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ORIGINAL ARTICLE

On *Sistotremastrum* and similar-looking taxa (Trechisporales, Basidiomycota)

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Abstract
The taxonomy of *Sistotremastrum* (Trechisporales, Basidiomycota) is revised based on morphology and DNA data. The genus is shown to be polyphyletic, and therefore it is split into two units—*Sistotremastrum* s. str. and *Sertulicium*, gen. nov. (typified with *Corticium niveocremeum*). *Sistotremastrum* s. str. is retained for eleven species of which eight are described as new while *Sertulicium* encompasses at least six species, including one new to science. Both of these genera are only distantly related to other representatives of the Trechisporales. Additionally, a new poroid neotropical species, *Porpomyces abiens* (*Hydnodontaceae*), is described as morphologically similar to some members of *Sistotremastrum* s. str.

Keywords Corticioid fungi · Phylogeny · Taxonomy · New taxa

Introduction

Sistotremastrum J. Erikss. is a genus of corticioid fungi typified with *S. suecicum* Litsch. ex J. Erikss. (Eriksson 1958). Initially introduced for two species, it has been gradually expanded to encompass smooth, effused basidiomycetes with clavate basidia producing four to six sterigmata and smooth, thin-walled, inamyloid basidiospores (Boidin and Gilles 1994; Telleria et al. 2013a, 2014). Recently, Gruhn et al. (2018) described two new *Sistotremastrum* species with a hydnoid hymenophore and constantly four-sterigmatic basidia and thus changed the present concept of the genus. As a consequence, the morphological delimitation of *Sistotremastrum* from *Brevicellicium* K.H. Larsson & Hjortstam and, partly, from *Trechispora* P. Karst. became obscure. Another yet persisting problem is the separation of *Sistotremastrum* from *Paullicorticium* J. Erikss., which has a similar set of microscopic characters (Eriksson et al. 1984). Oberwinkler (1965) moved *Sistotremastrum niveocremeum* (Höhn. & Litsch.) J. Erikss., one of the original species, to *Paullicorticium*, stressing similarities in basidial development. Larsson et al. (2004) included *Paullicorticium ansatum* Liberta in

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phylogenetic analyses of Agaricomycetes but were unable to place it in one of the clades currently recognized as orders. On the other hand, all *Sistotremastrum* species, including the generic type, have been found to be members of the Trechisporales (Larsson 2007; Telleria et al. 2013a, 2014; Gruhn et al. 2018). However, most *Paullicorticium* species have not yet been studied by DNA methods—in particular, *P. jacksonii* Liberta whose connection to *Sistotremastrum* was discussed in the older literature (Eriksson et al. 1978). In the present paper, we revise the generic limits of *Sistotremastrum* and similar-looking taxa, and investigate species diversity based on collections from different regions of Eurasia, as well as from North and South America.

Materials and methods

Morphological study

Type specimens and collections from herbaria H, O, LE, S, GB, MA, W, GENT, TRTC, LY, CWU, ANDA, MAN, SP, MG, SING, as well as from the private herbarium of the author JV were studied. Herbarium acronyms are given according to Thiers (2019). Microscopic methods follow Miettinen et al. (2018). All measurements were made from microscopic slides mounted in Cotton Blue (abbreviated as CB in descriptions below), using phase contrast and oil immersion lens (Leitz Diaplan microscope, × 1250 amplification). In total, 20–30 basidiospores, 20 basidia and subhymenial/subicular hyphae, and at least 10 basidioles and hyphidia were measured for each specimen studied. The following abbreviations are used in morphological descriptions: L—mean basidiospore length, W—mean basidiospore width, Q′—length/width ratio, Q—mean length/width ratio, n—number of measurements per specimens.

DNA extraction, amplification, and sequencing

DNA was extracted from herbarium specimens using the EZNA Forensic DNA kit (Omega Bio-tek) and AxyPrep Multisource Genomic DNA Miniprep kit (Axygen Biosciences, CA, USA) according to the manufacturer's instructions, except that 50 μl of the elution buffer was used in the elution step of the last one. The ribosomal ITS1–5.8S–ITS2 region was amplified and sequenced with the fungal specific primers ITS1F and ITS4B (Gardes and Bruns 1993). Sequences of nrLSU-rDNA were generated using primers LR0R, CTB6, LR5, and LR7 (Vilgalys and Hester 1990; Haynes et al. 1995). PCR products were visualized using agarose gel electrophoresis and Gel Red staining, and subsequently purified with the Fermentas Genomic DNA Purification Kit (Thermo Fisher Scientific, MA, USA). The resulting products were sequenced with an ABI model 3130 genetic analyzer (Applied Biosystems, CA, USA) and BigDye v.3.1 and ABI3730XL analyzer (Applied Biosystems) by Macrogen. The raw data were edited and assembled in MEGA 6 (Tamura et al. 2013).

Phylogenetic analyses

For this study, we generated 60 nrITS and 36 nrLSU sequences. All other sequences used in the analyses were downloaded from GenBank (Benson et al. 2018) or UNITE (Nilsson et al. 2018) (Table 1). All newly generated sequences were deposited in the INSDC.

Extremely high diversity of ITS sequences in the studied taxa precludes attempts to construct a reliable all-encompassing alignment for all *Sistotremastrum* spp. However, we could distinguish five alignable groups: *S. niveocremeum* complex, *S. suecicum* and its closest relatives, *S. aculeocrepitans* and its closest relatives, *S. fibrillosum* complex, and *S. rigidum–vigilans* clade. We found it reasonable to exclude *S. fibrillosum*, as well as newly described *S. rigidum* and *S. vigilans* from ITS analysis since molecular evidence provided by nrLSU analysis is sufficient for the purpose of our study. Therefore, we generated four alignments for this study: (1) nrLSU-alignment for the Trechisporales, (2) nrITS-alignment for *S. niveocremeum*, (3) nrITS-alignment limited to *S. suecicum* and its closest relatives, and (2) nrITS-alignment for *S. aculeocrepitans* and its closest relatives. The alignments were calculated through MAFFT 7.429 online server (https://mafft.cbrc.jp/alignment/server/) using the L-INS-I strategy (Katoh et al. 2017) and then manually adjusted. The alignments are deposited in TreeBASE (S25768).

For the genus-level analysis, a nrLSU dataset (1) was assembled with representatives of Trechisporales (65 sequences). The resulting tree was rooted with *Onnia leporina* and *Sphagnomphalia brevibasidiata* (Hymenochaetales) and *Sphaerobolus stellatus* (Geastrales, Phallomycetidae). This choice was guided by the current JGI Basidiomycota tree (https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;_FJDxL?organism=basidiomycota) where Trechisporales is recovered close to Hymenochaetales and Phallomycetidae. After removing unalignable, ambiguous alignment positions, the alignment length was 742 bp with 184 variable site patterns. The three ITS datasets were assembled similarly: the *S. niveocremeum* species complex alignment (2) contained 60 sequences and had the length of 329 bp with 40 variable site patterns after removing unalignable, ambiguous positions. The *S. suecicum* species complex analysis (3) contained 22 sequences, with alignment length of 508 bp with 13 variable site patterns after removing ambiguous positions. The *S. aculeocrepitans* species complex analysis (4) contained 22 sequences with the alignment length of 470 bp with 37 variable site patterns. All the ITS trees are midpoint-rooted.

We inferred phylogenetic trees with maximum likelihood (ML), maximum parsimony (MP), and Bayesian inference (BI) but show here only the latter since all trees show

Table 1 Sequences generated for the present study

Species	Specimen/herbarium	Geographic origin (ISO code)	Host	GenBank number	
				nrITS	nrLSU
Brevicellicium exile	Spirin 8370 (H)	US-WA	*Tsuga heterophylla*	MT002322	MT002338
B. olivascens	Spirin 4446 (H)	RU-NIZ	*Quercus robur*	MT002327	-
B. viridulum	Kotiranta 29271 (H)	RU-SAK	*Alnus hirsuta*	MN983275	-
Luellia cystidiata	Læssøe 13875 (GB)	DK	*Picea abies*	MW371211	MW371211
Porpomyces abiens	Vlasák 1808/16 (H)	GF	Hardwood	MN987945	MN987945
P. abiens	Vlasák 1808/39 (H)	GF	Hardwood	MN987942	MN987942
Pteridomyces galzinii	Bernicchia 8122 (GB)	IT	*Polystichum aculeatum*	MN937559	MN937559
Sertulicium granuliferum	Spirin 9296 (H)	RU-NIZ	*Populus tremula*	MT002321	-
S. granuliferum	LE 292194	RU-ORL	*Betula pendula*	MT002325	MT002333
S. granuliferum	LE 314053	RU-ORL	*Q. robur*	MT002313	MT002340
S. granuliferum	LE 314054	RU-ORL	*Q. robur*	MT002315	MT002342
S. granuliferum	LE 314055	RU-ORL	*B. pendula*	MT002314	MT002341
S. granuliferum	LE 314056	RU-ORL	*Q. robur*	MT002316	MT002343
S. granuliferum	LE 314057	RU-ORL	*Q. robur*	MT002312	MT002339
S. granuliferum	Kotiranta 26776 (H)	RU-TY	*Larix sibirica*	MT002323	-
S. granuliferum	CWU 4704	UA	*Salix alba*	MT002326	-
S. granuliferum	Miettinen 14813.2 (H)	US-MA	Cut bole	MT075854	-
S. granuliferum	Miettinen 16083 (H)	US-MA	Hardwood	MT002319	-
S. granuliferum	Miettinen 17272 (H)	US-MA	*Quercus* sp.	MT002330	-
S. granuliferum	Larsson 12282 (GB)	US-TN	Decayed wood	MN937560	MN937560
S. granuliferum	Larsson 12297 (GB)	US-TN	Decayed wood	MN937561	MN937561
S. jacksonii	Svantesson 699 (O)	NO	*Picea abies*	MN937562	MN937562
S. jacksonii	Spirin 10425 (H)	RU-LEN	*P. abies*	MN987943	MN987943
S. jacksonii	Miettinen 17141 (H)	US-NY	*Abies* sp.	MN987944	-
S. lateclavigerum	Spirin 13457	SI	*P. abies*	MW049161	-
S. niveocremeum	Van Autgaerden S-20 (GENT)	BE	Hardwood	MN947227	MN930920
S. niveocremeum	Miettinen 14925.3 (H)	FI	*Sorbus aucuparia* (?)	MT075855	-
S. niveocremeum	Söderholm 4050 (H)	FI	*Salix* sp.	MT075856	MT002334
S. niveocremeum	Larsson 13727 (GB)	FR	Hardwood	MN937563	MN937563
S. niveocremeum	Kotiranta 26267 (H)	RU-KRA	*Alnus sibirica*	MT075858	MT002337
S. vernale	Söderholm 3886 (H)	FI	*P. abies*	MT002311	MT664174
Sertulicium sp. 1	Spirin 5158 (H)	RU-KHA	*Corylus mandshurica*	MT075857	MT002344
Sistotremastrum aculeatum	Miettinen 10380.1 (H)	CN-YN	Hardwood (?)	MN991176	MW045423
S. aculeatum	Miettinen 13799.1 (ANDA)	ID-SB	Hardwood	MN988623	-
S. aculeatum	Dunaev KUN 1105 (H)	TH	Hardwood	MN991181	-
S. aculeicrepitans	Larsson 16097 (URM)	BR-PB	Hardwood	MN937564	MN937564
S. aculeicrepitans	Larsson 16478 (MG)	BR-PA	Hardwood	MN937565	-
S. confusum	Larsson 16004 (URM)	BR-PE	Hardwood	MN937567	MN937567
S. confusum	Larsson 16023 (URM)	BR-PE	Hardwood	MN937566	-
S. denticulatum	Motato-Vásquez 894 (SP)	BR-SP	Fallen branch	MN954694	MW045424
S. fibrillosum	Larsson 16988 (MG)	BR-PA	Hardwood	MN937568	MN937568
S. geminum	Miettinen 14333 (MAN)	ID-PB	*Intsia bijuga*	MN991177	MN991177
S. induratum	Spirin 8598 (H)	US-WA	*Abies grandis*	MT002324	MT664173
S. induratum	Spirin 8804 (H)	US-WA	*Picea sitchensis*	MT002318	-
S. mendax	J. Nordén 9579 (O)	NO	*P. abies*	MN937569	-
S. mendax	Larsson 12022 (O)	NO	*P. abies*	MN937570	MN937570
S. mendax	Miettinen 20946 (H)	RU-LEN	*P. abies*	MN991179	-

Table 1 (continued)

Species	Specimen/herbarium	Geographic origin (ISO code)	Host	GenBank number	
				nrITS	nrLSU
S. rigidum	Motato-Vásquez 833 (SP)	BR-SP	Fallen log	MN954693	MW045435
S. suecicum	Spirin 8932 (H)	CA-BC	*Pinus contorta*	MT002317	-
S. suecicum	Kunttu 5959 (H)	FI	*Pinus sylvestris*	MT075859	MT002335
S. suecicum	LE 295792	RU-ARK	*P. sylvestris*	MT002332	-
S. suecicum	Miettinen 14550.1 (H)	SE	*P. sylvestris*	MT075860	MT002336
S. suecicum	Larsson 11849 (GB)	SE	*P. abies* (?)	MN937571	MN937571
S. suecicum	Miettinen 14829 (H)	US-MA	Fallen branch	MT075861	-
S. suecicum	Miettinen 16061 (H)	US-MA	*Tsuga canadensis*	MT002328	-
S. suecicum	Miettinen 16618 (H)	US-MA	*Tsuga* sp./*Pinus* sp.	MT002331	-
S. vigilans	Fonneland 2011-78 (O)	NO	*P. abies*	MN937572	MN937572
S. vigilans	Spirin 10097 (H)	RU-LEN	*P. abies*	MN991178	-
S. vigilans	Spirin 8778 (H)	US-WA	*T. heterophylla*	MN991182	MN991182
Suillosporium cystidiatum	Spirin 3830 (H)	RU-KHA	*Picea ajanensis*	MN937573	MN937573

congruity of the phylogenetic signal. The best nucleotide substitution model was chosen with TOPALi 2.5 (Milne et al. 2008) based on the Akaike information criterion (AIC), which were GTR + G + I (nst = 6, rates = invgamma) for the nrLSU-dataset, GTR+G (nst = 6, rates = gamma) for the *S. niveocremeum* dataset, and F81 (nst = 1) for the *S. suecicum* dataset. The suggested models were implemented in the Bayesian phylogenetic analyses. We performed Bayesian inference with MrBayes 3.2 (Ronquist et al. 2012). In the analyses, three parallel runs with four chains each, temp = 0.2, were run for 3 million generations. All chains converged to <0.01 average standard deviation of split frequencies. A burn-in of 25% was used in the final analyses. Maximum likelihood (ML) analysis was performed in RAxML 7.2.8 (Stamatakis 2006) implemented in Geneious version 9.1.8 (http://www.geneious.com) (Kearse et al. 2012). Following models suggested by TOPALi 2.5, we preferred to use the GTR model with gamma correction (GTR GAMMA) in ML analysis. Bootstrapping was performed using the "Rapid bootstrapping" algorithm with the number of bootstrap replicates set as 1000. Maximum parsimony (MP) analysis was performed using SeaView version 4 (Gouy et al. 2010) with the ignoring all gap sites option. The number of bootstrap replicates was set as 1000.

Results

The nrLSU dataset encompasses all known genera of the Trechisporales as defined by Larsson et al. (2004) and Larsson (2007), with addition of *Pteridomyces* and *Suillosporium*. The overall topologies of the Trechisporales were highly similar (Fig. 1). They split the order into three strongly supported clades:

(A) the *Sistotremastrum* s. str. subclade (pp = 1, bs = 99%) includes the generic type, *S. suecicum*, and two unnamed closely related species (introduced below as *S. induratum* and *S. mendax*), all with six-sterigmatic basidia, plus eight more distantly related species with four-sterigmatic basidia (*S. aculeocrepitans*, *S. fibrillosum* and six new species);

(B) the *S. niveocremeum* subclade (pp = 1, bs = 100%) covers five species formerly considered as members of *Sistotremastrum* (except *P. jacksonii* and one unnamed taxon) but separated below into a new genus, *Sertulicium*. Morphological arguments for this solution are given in the taxonomic part of the present paper. *Sistotremastrum guttuliferum* is a younger synonym of *Trechispora granulifera*, and therefore designated as *Sertulicium granuliferum* in the phylogenetic trees; and

(C) the *Hydnodontaceae* clade (pp = 1, bs = 99%) covers ten genera currently recognized in the family (Larsson 2007; Liu et al. 2019). Among them, two sequences belong to an unnamed poroid fungus from French Guiana introduced below as *Porpomyces abiens*. Anatomically, its basidiocarps are confusingly similar to the four-sterigmatic *Sistotremastrum* species (i.e., *S. aculeocrepitans*, *S. fibrillosum*, and a number of new species described in this study) and differ from them mainly by a truly poroid hymenophore and smaller basidiospores. Sequences of three *Brevicellicium* species (including the generic type, *B. exile*) showing considerable morphological similarity to the four-sterigmatic *Sistotremastrum* species are also resolved in the *Hydnodontaceae*, in accordance to earlier

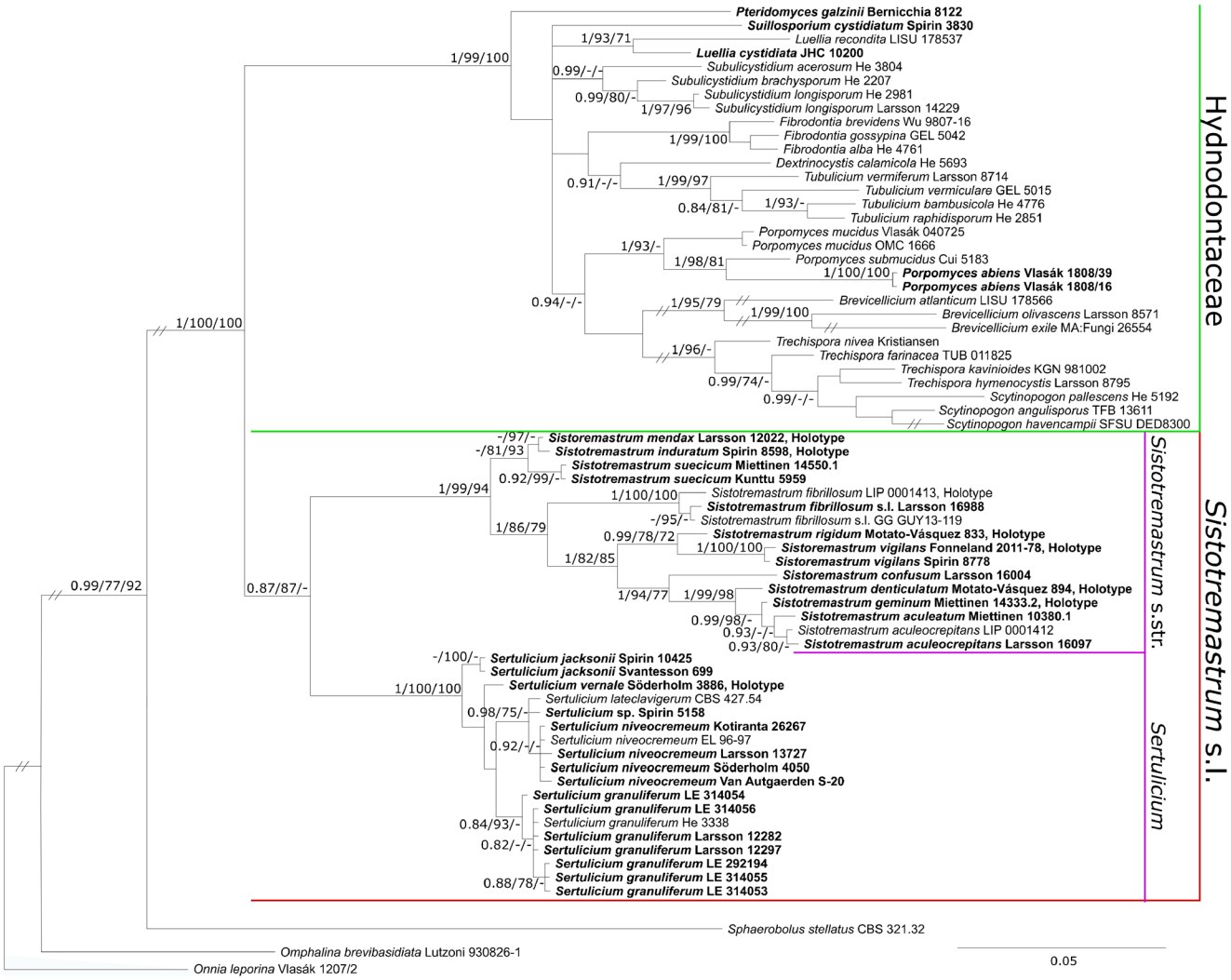

Fig. 1 Phylogenetic relationships of the Trechisporales inferred from nrLSU sequences using Bayesian analysis. A 50% majority rule consensus phylogram. Bayesian posterior probabilities, ML bootstrap, and MP bootstrap values are shown on nodes; branch lengths reflect estimated number of changes per site

studies (Larsson 2007; Telleria et al. 2013b). Morphological traits differentiating *Sistotremastrum* s. str. from *Brevicellicium* and *Trechispora* are discussed in the taxonomic part of this paper. As for the family-level rearrangement of *Sistotremastrum* and *Sertulicium*, we address this question to further studies with the use of additional genetic markers.

Additionally, three ITS datasets were constructed for the new genus *Sertulicium* and the *Sistotremastrum suecicum* and *S. aculeocrepitans* complexes to clarify species limits with the use of larger amount of ITS sequences. The ITS-based topology of *Sertulicium* (Fig. 2) indicates a presence of up to ten species in the genus of which we have named six. Furthermore, ITS sequences of *S. jacksonii* and *S. vernale* reveal some differences (up to 1.4%) between European and extra-European material. This may indicate that both species, as they are here delimited, actually contain more than one taxon. However, more samples and genetic markers are needed to solve this problem. The second ITS-based phylogeny is restricted to the *S. suecicum* complex (Fig. 3). It shows the presence of at least two more species (described below as *S. induratum* and *S. mendax*) morphologically similar and phylogenetically close to the generic type of *Sistotemastrum*. The third ITS-based phylogram shows phylogenetic relationships of *S. aculeocrepitans* and up to five closely related species. Of them, three are described as new to science, all having four-sterigmatic basidia (*S. aculeatum*, *S. denticulatum*, and *S. geminum*) (Fig. 4). Four remaining *Sistotremastrum* species (*S. confusum*, *S. fibrillosum*, *S. rigidum*, and *S. vigilans*) dealt with in the present paper are represented in the nrLSU phylogeny (Fig. 1). Their ITS sequences are available in GenBank (Table 1). Sequenced specimens are marked by asterisk.

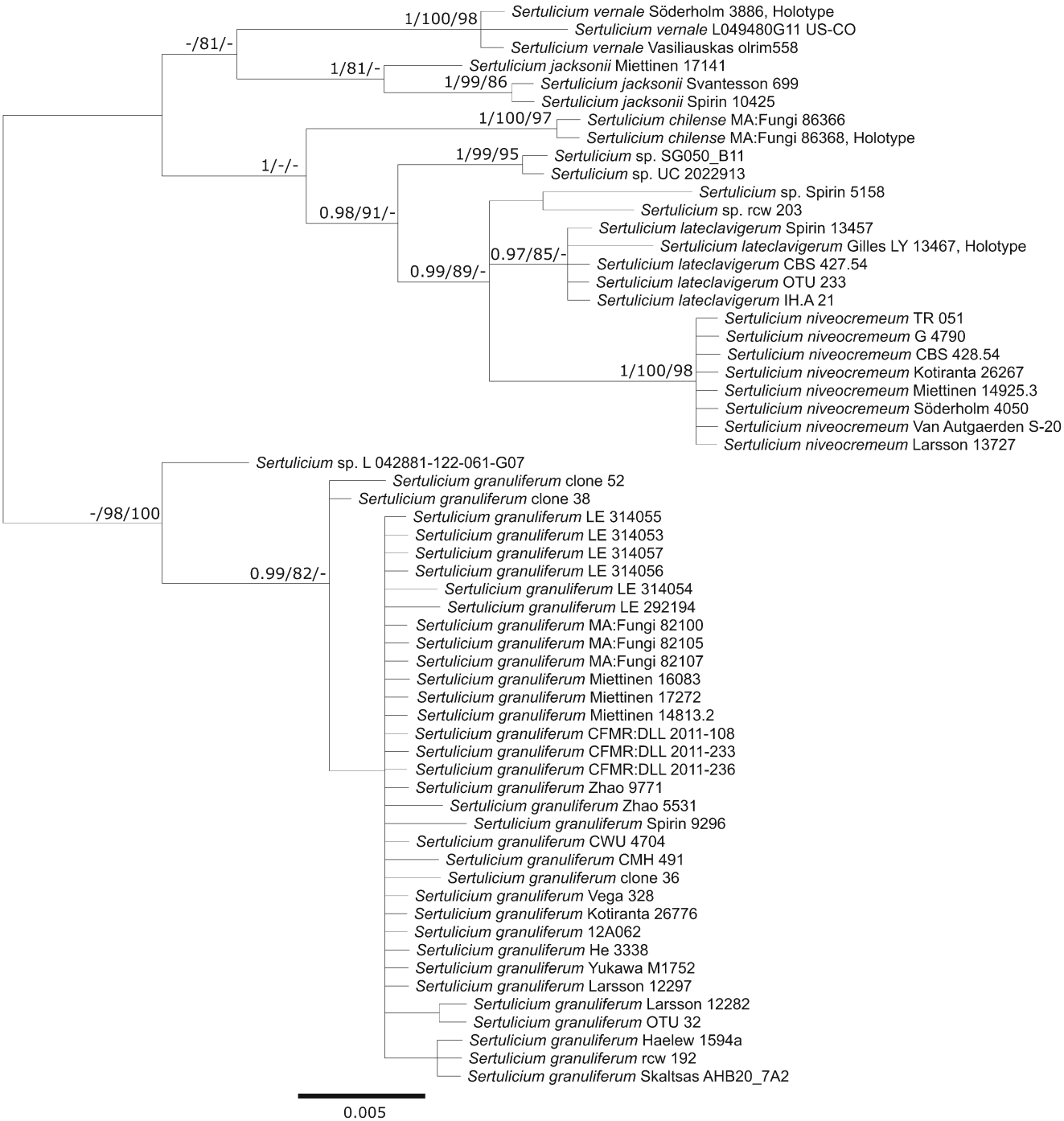

Fig. 2 Phylogenetic relationships of *Sertulicium* inferred from ITS sequences using Bayesian analysis. A 50% majority rule consensus phylogram. Bayesian posterior probabilities, ML bootstrap, and MP bootstrap values are shown on nodes; branch lengths reflect estimated number of changes per site

Taxonomy

Porpomyces Jülich, Persoonia 11: 425, 1982.

The genus was initially introduced as monotypic, encompassing only the type, *Porpomyces mucidus* (Pers.) Jülich (Jülich 1982). Larsson (2001) showed it is related to *Trechispora*. Another species, *P. submucidus* F. Wu & C.L. Zhao, was recently described from China (Wu et al. 2015). Here, we introduce the third representative of the genus, *P. abiens* from South America. From *P. mucidus* and *P. submucidus*, *P. abiens* differs by distinctly thick-walled and tightly arranged hyphae in subiculum and trama. This hyphal structure is clearly different from the loosely arranged, rather delicate, thin- or only slightly thick-walled hyphae of

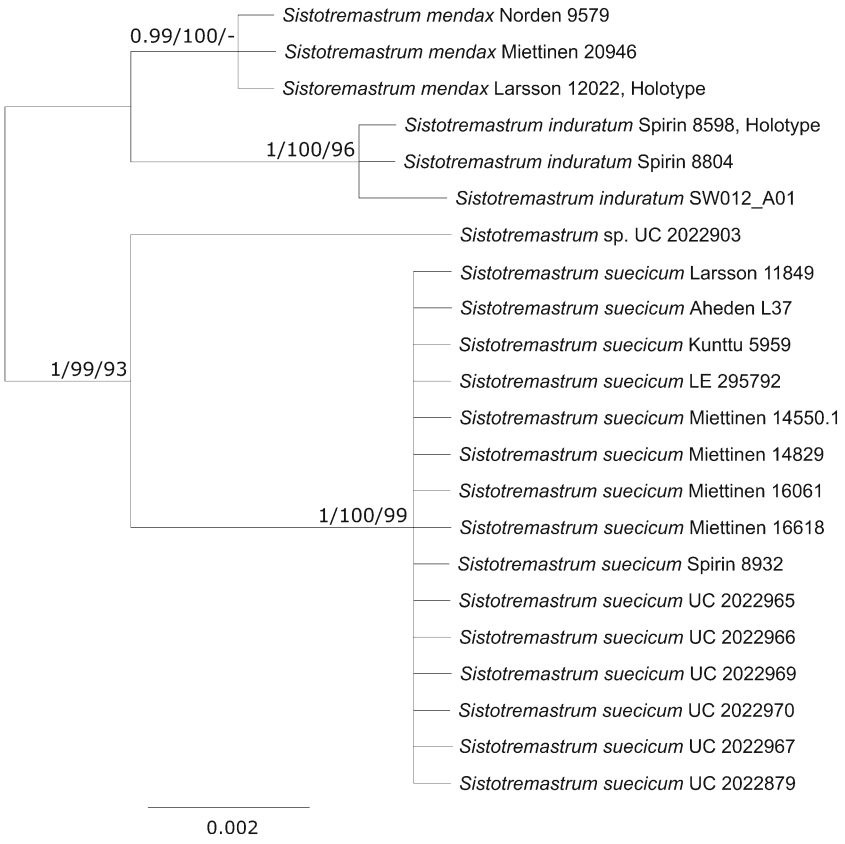

Fig. 3 Phylogenetic relationships of *Sistotremastrum suecium* and closely related taxa inferred from ITS sequences using Bayesian analysis. A 50% majority rule consensus phylogram. Bayesian posterior probabilities, ML bootstrap, and MP bootstrap values are shown on nodes; branch lengths reflect estimated number of changes per site

Fig. 4 Phylogenetic relationships of *Sistotremastrum aculeocrepitans* and closely related taxa inferred from ITS sequences using Bayesian analysis. A 50% majority rule consensus phylogram. Bayesian posterior probabilities, ML bootstrap, and MP bootstrap values are shown on nodes; branch lengths reflect estimated number of changes per site

P. mucidus and *P. submucidus*. The two latter species have thin-walled basidia and no sterile hymenial elements while basidia are slightly thick-walled in a senescent hymenium of *P. abiens* and hyphidia are present. Rather tough basidiocarps consisting of predominantly thick-walled hyphae and short, tardily thick-walled basidia of *P. abiens* are reminiscent of hydnoid-semiporoid *Sistotremastrum* species, i.e., *S. aculeatum*, *S. aculeocrepitans*, and *S. denticulatum*. The only reliable anatomical traits differentiating them from *P. abiens* are their suburniform basidia and somewhat larger basidiospores. Moreover, no truly poroid species are so far known in *Sistotremastrum* s. str.

Porpomyces abiens Vlasák & Spirin, **sp. nov**.—Figs. 5 and 6

MB 833939

Holotype. French Guiana. Remire-Montjoly: Lac du Rorota, rotten angiosperm wood, 23.VIII.2018 *Vlasák 1808/16** (H 7009714).

Etymology. *Abiens* (Lat., part. from *abeo*)—departing, deviating.

Basidiocarps effused, first soft-floccose, then rather tough, covering several cm, 0.2–1 mm thick. Hymenial surface pale cream-colored to yellowish or pale ochraceous, poroid, pores angular to sinuous, partly fusing together, strongly elongated on sloping substrate, 6–9 per mm, with thin, entire dissepiments. Margin white to pale cream-colored, fibrillose or compact, in some portions with thin, white, pronounced hyphal strands.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae slightly to distinctly thick-walled, (2.2–) 2.7–7.3 (–7.8) μm in diam. (n = 20/1), interwoven or in subparallel bundles, often distinctly inflated (up to 10 μm); some hyphae encrusted by densely distributed thorn-like crystals or subglobose resinous globules. Tramal hyphae distinctly thick-walled, rather tightly arranged, interwoven to subparallel, occasionally anastomosing, partly glued together, (2.2–) 2.8–5.8 (–6.4) μm in diam. (n = 40/2), sometimes inflated near septa; some hyphae encrusted by densely distributed subglobose resinous globules. Subhymenial hyphae thin- to slightly thick-walled, mostly short-celled and distinctly inflated, (2.0–) 2.2–5.2 (–5.4) μm in diam. (n = 40/2). Rhomboid or prismatic crystals occasionally present among subicular or tramal hyphae, up to 15 μm in widest dimension, solitary or in large groups. Hyphidia rarely present, 10–12 × 3.5–5 μm. Basidia subglobose to barrel-shaped or shortly clavate, 2–4-spored, (4.8–) 4.9–7.9 (–8.0) × (3.4–) 3.7–4.8 (–5.0) μm (n = 30/2), senescent basidia slightly thick-walled. Basidioles subglobose to globose, 4–5 × 4–4.5 μm. Basidiospores broadly cylindrical to ellipsoid, more rarely somewhat tapering to the apex (lacrymoid), (2.3–) 2.5–3.2 (–3.3) × (1.6–) 1.7–2.2 (–2.3) μm (n = 60/2), L = 2.87–2.94, W = 1.98–2.00, Q = 1.46–1.47, contents homogeneous and CB (+).

Remarks. *Porpomyces abiens* has been detected in three localities in French Guiana. It seems to be a saprotrophic species occurring on wood remnants, various debris and soil.

Specimens examined. French Guiana. Remire-Montjoly: Lac du Rorota, hardwood, 23.VIII.2018 *Vlasák 1808/39** (H, JV). Roura: Natural Reserve of Kaw, Patawa Lodge, on soil between the roots of uprooted tree, 31.VIII.2018 *Vlasak 1808/146* (JV), Amazon Lodge, rotten hardwood log, 4.IX.2019 *Vlasák 1909/29** (JV).

Sertulicium Spirin, Volobuev & K.H. Larss., **gen. nov**.

MB 833941

Etymology. *Sertulum* (Lat., noun)—a small chaplet.

Basidiocarps effused, very thin to rather thin (usually up to 0.1 mm thick), pruinose or waxy. Hymenophore smooth. Hyphal structure monomitic; all hyphae clamped, CB (+). Cystidia mostly absent, hyphidia rarely present, simple. Basidia clavate, with 4–6 sterigmata, normally not collapsing at the apex. Basidiospores thin-walled (but the wall distinct), narrowly ellipsoid to cylindrical, inamyloid, acyanophilous, contents homogeneous and CB (+). On rotten wood of deciduous trees and conifers.

Generic type. *Corticium niveocremeum* Höhn. & Litsch.

Morphological differences between *Sertulicium* and *Sistotremastrum* s. str. cannot be easily grasped due to the extreme anatomical simplicity of their representatives. Nevertheless, some distinguishing characters are indicated here awaiting more in-depth analysis in the future. First, all but one *Sertulicium* spp. are extremely thin fungi consisting of a few subicular hyphae and the overlying subhymenium. The subicular hyphae are scattered; i.e., they do not produce hyphal strands so characteristic for most *Sistotremastrum* s. str. species studied by us. The only exception is *Sertulicium granuliferum*, having the most elaborate fructifications in the genus. Its basidiocarps start their development as radially arranged hyphal bundles becoming quickly covered by randomly arranged hyphae and finally indiscernible. In contrast, in *Sistotremastrum* s. str. subicular hyphal strands can be detected even in senescent basidiocarps if hyphae are not totally collapsed. Second, basidia in all *Sertulicium* spp. bear up to six sterigmata while at least some *Sistotremastrum* s. str. species are strictly four-sterigmatic. Moreover, apical parts of basidia in the latter genus often collapse, and hymenial cells of this kind dominate in well-developed and in senescent basidiocarps. Such apically collapsing basidia may occur in *Sertulicium* spp., too, but they are as a rule rare. Finally, all *Sertulicium* spp. have a smooth hymenial surface while about a half of the currently

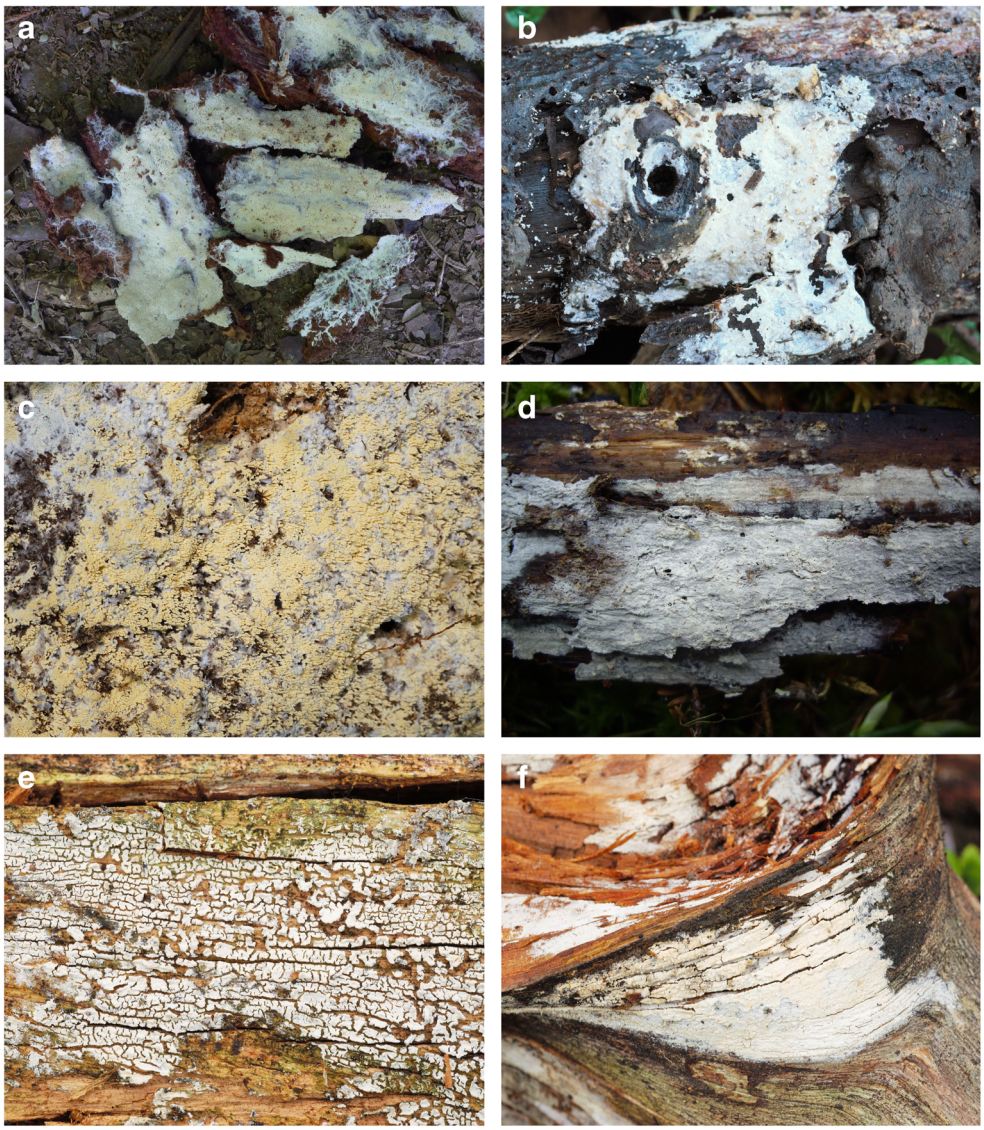

Fig. 5 Basidiocarps of **a** *Porpomyces abiens* (holotype), **b** *Sertulicium granuliferum* (Miettinen 23459), **c** *Sistotremastrum aculeatum* (holotype), **d** *S. mendax* (Spirin 11208), **e** *S. suecicum* (Miettinen 13310), and **f** *S. suecicum* (senescent basidiocarps) (Miettinen 14548)

known *Sistotremastrum* spp. have a hydnoid hymenophore.

Sertulicium chilense (Telleria, M. Dueñas & M.P. Martín) Spirin & Volobuev, **comb. nov**.

≡ *Sistotremastrum chilense* Telleria, M. Dueñas & M.P. Martín, Phytotaxa 158: 94, 2014 (as '*chilensis*').

MB 833942

Sistotremastrum chilense was described from Patagonia (Telleria et al. 2014) as a relative of *S. guttuliferum* (see under *Sertulicium granuliferum* below). From the latter species, it differs primarily in having long-celled subhymenial hyphae (vs. short-celled and somewhat inflated in *S. granuliferum*). DNA data confirm its placement in *Sertulicium*.

Sertulicium granuliferum (Hallenb.) Spirin & Volobuev, **comb. nov**.—Figs. 5 and 10

MB 833943

≡ *Trechispora granulifera* Hallenb., Iranian J. Plant Path. 14: 77, 1978. Holotype. Iran. Gilan: Asalem, *Parrotia persica*, 16.VII.1976 *Hallenberg 1885* (GB 23442, studied).

= *Sistotremastrum guttuliferum* Melo, M. Dueñas, Telleria & M.P. Martín, Mycological Progress 12: 688, 2013. Holotype. Portugal. Madeira: Santana, decayed wood, 19.X.2006 *Telleria 16566** (MA F82105, studied).

Basidiocarps effused, initially reticulate, soft-pellicular, then continuous, waxy, covering several cm, 0.05–0.1 mm thick. Hymenial surface first cream-colored, later yellowish to pale ochraceous, smooth or indistinctly tuberculate,

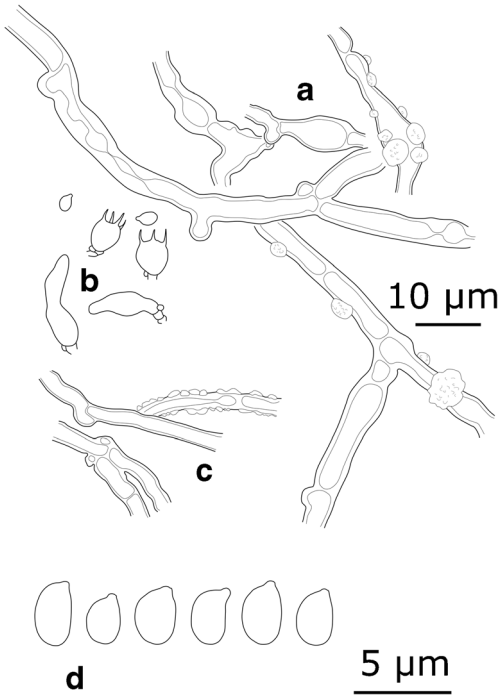

Fig. 6 Microscopic structures of *P. abiens* (holotype). **a** Subicular hyphae. **b** Hymenial cells. **c** Tramal hyphae. **d** Basidiospores

occasionally cracking in senescent basidiocarps. Margin first pruinose, later compact and rather sharply delimited. Small white patches spread at the marginal areas of young specimens, consisting of crystal agglomerations.

Hyphal structure monomitic; hyphae clamped, quickly collapsing. Subicular hyphae subparallel (juvenile specimens) to interwoven, thin- or slightly thick-walled, branched mostly at right angles, (3.0–) 3.1–6.5 (–6.9) µm in diam. (n = 100/5). Subhymenial hyphae thin-walled, densely arranged, some short-celled and slightly inflated, (2.2–) 2.3–4.2 (–4.6) µm in diam. (n = 100/5). Hyphidia occasionally present, embedded, simple, 3–4 µm in diam. Basidia clavate, 4–6-spored, gradually tapering to the basal part, (11.3–) 13.6–30.2 (–32.7) × (4.3–) 4.4–6.6 (–6.7) µm (n = 100/5). Basidioles clavate to bladder-shaped, (7.3–) 9.1–13.8 (–14.6) × (4.7–) 4.8–7.2 (–7.3) µm (n = 30/2). Basidiospores cylindrical, straight, rarely slightly curved, (4.8–) 4.9–7.3 (–8.0) × (2.3–) 2.5–3.3 (–3.5) µm (n = 270/9), L = 5.40–6.76, W = 2.78–3.07, Q = 1.81–2.41.

Remarks. This species was introduced as a member of *Trechispora* due to some morphological similarity to the smooth-spored members of that genus (i.e., *Trechispora cohaerens* group) (Hallenberg 1978). Larsson (1992) found clavate basidia with 4–5 sterigmata in the type collection and thus pointed towards possible affinities with *Sistotremastrum*. After rechecking the type, as well as morphological and DNA studies of newly collected material, we conclude that *T. granulifera* is an older name for the species recently introduced as *Sistotremastrum guttuliferum* (Telleria et al. 2013a). Consequently, a new combination is proposed.

Sertulicium granuliferum differs from the similar-looking *S. niveocremeum* in having thicker and softer basidiocarps with a well-developed subicular layer and smaller basidiospores (Table 2).

Sertulicium granuliferum is widely distributed in temperate Eurasia. It seems to be not rare along the eastern coast of Canada and the USA, and its distribution in North America stretches to the central part of Mexico. All but one specimen came from wood remnants of deciduous trees, mostly from decayed wood but a few from still corticated, rather tough branches or logs. One specimen from Ethiopia is morphologically indistinguishable from other collections studied by us and therefore accepted here as *S. granuliferum*. Three other collections from Africa (Kenya and Tanzania) are microscopically identical to *S. granuliferum* but strikingly different macroscopically due to a well-developed, distinctly fibrillose margin. They may represent yet another species in this genus and thus treated as *Sertulicium* aff. *granuliferum* under Specimens examined. ITS regions of two published *Sistotremastrum* genomes (Nagy et al. 2016; *Sistotremastrum niveocremeum* LOAV00000000.1 and *Sistotremastrum suecicum* SRA:SRR1800527.68548550.2) appear to be conspecific and belong to *Sertulicium granuliferum*.

Specimens examined. Belgium. Oost-Vlaanderen: Kluisbergen, Kluisbos, deciduous wood, 20.II.2017 *Schoutteten 17-021, 17-022* (GENT), 7.III.2017 *Schoutteten 17-108* (GENT). Canada. Québec: Outaouais, Gatineau Nat. Park, angiosperm, 17.X.1967 *Eriksson 9155* (GB), *Acer* sp., 17.X.1967 *Eriksson 9177* (GB). Ethiopia. Shoa Prov.: Shashemene, dead hardwood twig, 18.VII.1990 *Ryvarden 28557* (O). Germany. Nordrhein-Westphalen: Essen, Werden, deciduous wood, 6.I.2020 *Miettinen 23459* (H). Italy. Lombardy: Varese, Valganna, San Gemolo, *Fraxinus excelsior*, 14.X.2019 *Spirin 13657* (H). Mexico. Vera Cruz: Barranca de Pescado, angiosperm, 26.IX.1985 *Ryvarden 23449* (O). Russia. Kemerovo Reg.: Novokuznetsk Dist., Kuzedeevo, *Betula* sp., 3.IX.2011 *Kotiranta 28540* (H), *Salix caprea*, 4.IX.2011 *Kotiranta 28597* (H). Leningrad Reg.: Boksitogorsk Dist., Chagoda, *Alnus incana*, 9.V.2018 *Spirin 11877* (H). Nizhny Novgorod Reg.: Bogorodsk Dist., Krastelikha, *Tilia cordata*, 14.IX.2010 *Spirin 3503* (H), *Q. robur*, 2.X.2015 *Spirin 9898*, *9899*, *9910* (H), 17.VII.2016 *Spirin 10310, 10313, 10315* (H), 5.V.2018 *Spirin 11862* (H); Lukoyanov Dist., Panzelka, *Padus avium*, 17.VIII.2015 *Spirin 9479* (H), 9.VIII.2016 *Spirin 10577* (H), Razino, *Populus tremula*, 15.VIII.2015 *Spirin 9296** (H), *Q. robur*, 10.VIII.2016 *Spirin 10605* (H), *T. cordata*, 23.VII.2018 *Spirin 12006* (H), Sanki, *Acer platanoides*, 20.VIII.2015 *Spirin 9658* (H); Pavlovo Dist., Chudinovo, *P. tremula*, 3.X.2015 *Spirin 9977* (H), 15.VII.2016 *Spirin 10281, 10284* (H), *T. cordata*, 15.VII.2016 *Spirin 10263* (H). Oryol Reg.: Krasnozorensky Dist., Malinovo, *Q. robur*, 7.X.2012 *Volobuev* (LE 314056*); Novoderevenkovsky

Table 2 Basidiospore dimensions of *Porpomyces* and *Sistotremastrum* s. lato species. Species name and basidiospore dimensions for a given taxon are presented in bold

Species/specimen	L′	L	W′	W	Q′	Q	n
Porpomyces abiens	**(2.3) 2.5–3.2 (3.3)**	**2.91**	**(1.6) 1.7–2.2 (2.3)**	**1.99**	**(1.2) 1.3–1.7 (1.8)**	**1.47**	**60**
holotype	(2.4) 2.5–3.2 (3.3)	2.94	(1.6) 1.7–2.2	2.00	(1.2) 1.3–1.7 (1.8)	1.47	30
Vlasák 1808/39	(2.3) 2.6–3.2 (3.3)	2.87	(1.7) 1.8–2.2 (2.3)	1.98	(1.3) 1.4–1.6 (1.7)	1.46	30
Sertulicium granuliferum	**(4.8) 4.9–7.3 (8.0)**	**5.75**	**(2.3) 2.5–3.3 (3.5)**	**2.90**	**(1.5) 1.6–2.4 (2.5)**	**2.02**	**270**
Kotiranta 26776	5.1–6.7 (6.8)	5.70	(2.6) 2.7–3.2 (3.3)	2.88	(1.6) 1.8–2.2 (2.3)	1.98	30
Larsson 12282	(5.0) 5.1–6.0 (6.1)	5.46	(2.7) 2.8–3.2 (3.3)	3.02	(1.6) 1.7–2.0 (2.1)	1.81	30
LE 299057	(4.8) 4.9–6.0 (6.1)	5.40	(2.5) 2.6–3.2	2.83	(1.6) 1.7–2.1 (2.2)	1.91	30
Miettinen 16083	(6.0) 6.1–7.3 (8.0)	6.76	(2.7) 2.8–3.3 (3.5)	3.07	(1.8) 2.0–2.4	2.21	30
Spirin 3503	(5.1) 5.2–6.2 (6.3)	5.82	(2.6) 2.7–3.1 (3.2)	2.85	(1.8) 1.9–2.3 (2.4)	2.04	30
Spirin 9296	5.2–6.5 (7.0)	5.95	(2.6) 2.7–3.2	2.87	(1.6) 1.8–2.4 (2.5)	2.41	30
Spirin 9898	(4.9) 5.0–6.1 (6.2)	5.46	(2.6) 2.7–3.2 (3.3)	2.86	(1.6) 1.7–2.1 (2.2)	1.92	30
Spirin 9977	(4.8) 5.1–6.6 (7.2)	5.63	(2.6) 2.7–3.3 (3.5)	2.97	(1.5) 1.6–2.2 (2.3)	1.91	30
Telleria 16566	(4.9) 5.0–6.1 (6.2)	5.56	(2.3) 2.5–3.1 (3.3)	2.78	(1.7) 1.8–2.2 (2.3)	2.00	30
S. jacksonii	**(5.1) 5.2–8.2 (8.6)**	**6.60**	**(2.7) 2.8–4.1 (4.2)**	**3.29**	**(1.5) 1.6–2.6 (2.7)**	**2.02**	**170**
holotype	(6.1) 6.2–8.0 (8.2)	7.13	(2.7) 2.8–3.2 (3.3)	2.99	2.2–2.6 (2.7)	2.39	20
Bernicchia 5464	(5.3) 5.7–7.3 (7.8)	6.52	(3.2) 3.3–4.1 (4.2)	3.66	(1.5) 1.6–2.1 (2.2)	1.79	30
Laurila 3256b	(5.2) 5.3–7.2	6.43	(2.7) 2.8–3.8 (4.0)	3.23	(1.8) 1.9–2.5 (2.6)	2.00	30
Miettinen 17141.2	(6.0) 6.1–8.2 (8.6)	6.96	3.0–3.4 (3.5)	3.21	(1.9) 2.0–2.5	2.17	30
Spirin 10425	(5.2) 5.6–7.4 (8.0)	6.49	(2.8) 2.9–3.8 (3.9)	3.30	(1.6) 1.7–2.3 (2.6)	1.97	30
Svantesson 699	(5.1) 5.2–6.8 (7.1)	6.08	(3.0) 3.1–3.9 (4.0)	3.36	(1.5) 1.6–1.9 (2.3)	1.81	30
S. lateclavigerum	**(4.3) 4.6–7.2 (7.3)**	**5.57**	**(2.1) 2.2–3.2**	**2.71**	**(1.7) 1.8–2.4 (2.5)**	**2.07**	**60**
holotype	(4.9) 5.0–7.2 (7.3)	5.82	(2.5) 2.6–3.2	2.84	(1.7) 1.8–2.3 (2.4)	2.05	30
Spirin 13457	(4.3) 4.6–6.2 (7.2)	5.32	(2.1) 2.2–3.0 (3.1)	2.57	(1.7) 1.8–2.4 (2.5)	2.09	30
S. niveocremeum	**(5.2) 5.5–8.6 (9.8)**	**6.86**	**(2.6) 2.7–4.2 (4.3)**	**3.25**	**(1.6) 1.7–2.4 (2.6)**	**2.12**	**120**
holotype	(5.2) 5.5–7.8 (9.8)	6.62	(2.6) 2.7–3.6 (4.3)	3.12	(1.7) 1.9–2.4 (2.5)	2.12	30
Kotiranta 26267	(5.7) 6.0–7.4 (7.6)	6.55	(2.7) 2.8–3.4 (3.5)	3.08	(1.9) 2.0–2.3 (2.5)	2.13	30
Miettinen 14925.3	(6.0) 6.1–8.6 (9.2)	7.46	(3.0) 3.1–3.6 (3.8)	3.33	(1.7) 1.8–2.4 (2.6)	2.24	30
Söderholm 4050	(6.0) 6.1–7.7 (7.8)	6.79	(3.0) 3.1–4.2 (4.3)	3.46	(1.6) 1.7–2.2 (2.3)	1.97	30
S. vernale	**(5.7) 5.8–8.2 (8.3)**	**6.96**	**(2.8) 2.9–3.8 (3.9)**	**3.30**	**(1.6) 1.8–2.5 (2.9)**	**2.12**	**60**
holotype	(5.7) 6.1–8.2 (8.3)	7.02	(2.8) 2.9–3.8	3.28	(1.6) 1.8–2.5 (2.9)	2.15	30
Spirin 14244	(5.7) 5.8–8.0 (8.1)	6.90	(2.9) 3.0–3.8 (3.9)	3.31	(1.6) 1.8–2.3 (2.4)	2.09	30
Sistotremastrum aculeatum	**(4.1) 4.2–6.2 (6.8)**	**5.03**	**(2.1) 2.2–3.1 (3.3)**	**2.58**	**(1.5) 1.6–2.4 (2.7)**	**1.97**	**120**
holotype	(4.1) 4.2–6.2 (6.8)	5.07	(2.2) 2.3–3.1 (3.3)	2.65	(1.5–)1.6–2.4 (2.7)	1.94	60
Dunaev KUN1105d	4.2–5.3 (5.4)	4.98	(2.1) 2.2–3.0 (3.1)	2.60	(1.6–)1.7–2.4 (2.5)	1.94	30
Miettinen 10380.1	(4.2) 4.3–6.1 (6.2)	5.05	(2.2) 2.3–2.8 (3.0)	2.50	1.8–2.2 (2.3)	2.03	30
S. aculeocrepitans	**(4.0) 4.1–5.6 (5.8)**	**4.77**	**(2.1) 2.2–2.8 (2.9)**	**2.33**	**1.8–2.5 (2.6)**	**2.06**	**60**
Larsson 16097	(4.4) 4.5–5.6 (5.8)	5.10	(2.1) 2.2–2.8 (2.9)	2.35	(1.8) 1.9–2.5 (2.6)	2.19	30
Larsson 16478	(4.0) 4.1–5.0 (5.1)	4.44	(2.1) 2.2–2.6 (2.7)	2.30	1.8–2.1 (2.2)	1.93	30
S. confusum	**(5.3) 5.7–7.6 (7.9)**	**6.56**	**2.9–3.9 (4.0)**	**3.24**	**(1.7) 1.8–2.3 (2.6)**	**2.03**	**60**
holotype	(5.3) 5.7–7.3 (7.8)	6.54	2.9–3.4 (3.8)	3.16	(1.7) 1.8–2.3 (2.6)	2.07	30
Larsson 16004	(5.3) 5.7–7.6 (7.9)	6.57	3.0–3.9 (4.0)	3.32	(1.7) 1.8–2.3 (2.4)	1.99	30
S. denticulatum	**(3.9) 4.0–5.3 (5.4)**	**4.51**	**(2.0) 2.1–3.0 (3.1)**	**2.48**	**(1.5) 1.6–2.3 (2.4)**	**1.83**	**30**
holotype	(3.9) 4.0–5.3 (5.4)	4.51	(2.0) 2.1–3.0 (3.1)	2.48	(1.5) 1.6–2.3 (2.4)	1.83	30
S. fibrillosum	**(4.0) 4.2–5.2 (5.6)**	**4.72**	**(2.1) 2.2–2.9 (3.0)**	**2.53**	**(1.6–)1.7–2.1 (2.2)**	**1.88**	**20**
Larsson 16988	(4.0) 4.2–5.2 (5.6)	4.72	(2.1) 2.2–2.9 (3.0)	2.53	(1.6–)1.7–2.1 (2.2)	1.88	20
S. geminum	**(3.8) 3.9–5.2 (5.5)**	**4.28**	**(1.9) 2.0–2.6 (2.9)**	**2.24**	**(1.7) 1.8–2.2 (2.3)**	**1.92**	**30**
holotype	(3.8) 3.9–5.2 (5.5)	4.28	(1.9) 2.0–2.6 (2.9)	2.24	(1.7) 1.8–2.2 (2.3)	1.92	30
S. induratum	**(4.0) 4.1–5.3 (5.8)**	**4.55**	**(2.5) 2.6–3.1 (3.2)**	**2.83**	**1.4–1.8 (1.9)**	**1.62**	**60**

Table 2 (continued)

Species/specimen	L′	L	W′	W	Q′	Q	n
holotype	(4.1) 4.2–5.3 (5.8)	4.73	(2.5) 2.6–3.0	2.79	(1.5) 1.6–1.8 (1.9)	1.70	30
Spirin 8804	(4.0) 4.1–5.0 (5.1)	4.37	(2.5) 2.6–3.1 (3.2)	2.86	1.4–1.8 (1.9)	1.53	30
S. mendax	**(4.0) 4.2–7.0 (7.2)**	**5.27**	**(2.4) 2.5–3.5 (3.6)**	**2.93**	**(1.3) 1.4–2.1 (2.3)**	**1.80**	**180**
holotype	(4.7) 4.8–6.2	5.60	(2.7) 2.9–3.5 (3.6)	3.09	(1.6) 1.7–2.1 (2.3)	1.82	30
Larsson 12022	(4.6) 4.8–5.6	5.12	(2.6) 2.7–3.0 (3.1)	2.85	(1.6) 1.7–1.9	1.80	30
Nordén 9579	(4.7) 4.8–5.8 (6.0)	5.33	(2.6) 2.7–3.1 (3.2)	2.93	(1.6) 1.7–2.0 (2.1)	1.82	30
Spirin 10060	(5.0) 5.1–7.0 (7.2)	5.71	(2.6) 2.7–3.2 (3.3)	2.93	1.7–2.3 (2.4)	1.95	30
Spirin 10107	(4.2) 4.3–5.9 (6.1)	5.11	(2.7) 2.8–3.2 (3.5)	3.00	(1.3) 1.4–1.9 (2.0)	1.71	30
Vlasák 1110/14.1	(4.0) 4.2–5.4 (5.5)	4.75	(2.4) 2.5–3.0	2.76	(1.4) 1.5–1.9	1.72	30
S. rigidum	**(3.8) 4.0–5.1 (5.2)**	**4.44**	**2.0–2.5 (2.7)**	**2.22**	**(1.6) 1.7–2.2 (2.3)**	**2.01**	**30**
holotype	(3.8) 4.0–5.1 (5.2)	4.44	2.0–2.5 (2.7)	2.22	(1.6) 1.7–2.2 (2.3)	2.01	30
S. suecicum	**(4.1) 4.2–6.2 (6.3)**	**4.90**	**(2.1) 2.2–3.1 (3.2)**	**2.53**	**(1.5) 1.6–2.4 (2.5)**	**1.93**	**180**
holotype	(4.8) 5.1–6.2 (6.3)	5.55	(2.4) 2.5–3.1 (3.2)	2.80	(1.7) 1.8–2.2 (2.3)	1.99	30
Kunttu 5959	(4.1) 4.2–5.2	4.70	2.2–2.8 (2.9)	2.52	(1.6) 1.7–2.1 (2.2)	1.88	30
Larsson 11849	(4.1) 4.2–5.7 (5.8)	4.91	(2.1) 2.2–2.9	2.42	(1.7) 1.8–2.4 (2.5)	2.05	30
Miettinen 11044	(4.5) 4.6–5.9 (6.1)	5.12	2.2–2.9 (3.0)	2.50	(1.7) 1.8–2.3 (2.5)	2.06	30
Miettinen 14550.1	(4.1) 4.2–5.1 (5.3)	4.60	2.2–2.9 (3.0)	2.52	(1.5) 1.6–2.0 (2.1)	1.83	30
Spirin 8932	(4.1) 4.2–5.3 (5.8)	4.56	(2.1) 2.2–2.9 (3.0)	2.42	(1.7) 1.8–2.1 (2.2)	1.89	30
S. vigilans	**(6.1) 6.3–11.2 (11.4)**	**8.68**	**(3.0) 3.1–5.4 (6.2)**	**4.35**	**(1.6) 1.7–2.5 (2.6)**	**2.01**	**150**
holotype	(7.0) 7.2–9.1 (9.4)	8.09	(3.9) 4.0–5.2 (5.8)	4.49	(1.6) 1.7–2.0 (2.1)	1.81	30
Eriksson 9106	(8.0) 8.3–10.5 (10.6)	9.34	(3.8) 4.0–5.0 (5.1)	4.44	(1.8) 1.9–2.2 (2.3)	2.11	30
Fonneland 2011-77	(8.1) 8.8–11.2 (11.4)	9.95	(4.0) 4.1–5.1 (5.2)	4.50	(1.8) 1.9–2.5 (2.6)	2.22	30
Häyrén 1934	(7.7) 7.8–10.3 (10.9)	8.61	(4.1) 4.2–5.4 (6.2)	4.69	(1.7) 1.8–2.0 (2.1)	1.84	30
Spirin 8778	(6.1) 6.3–8.8 (8.9)	7.43	(3.0) 3.1–4.3 (4.5)	3.64	(1.7) 1.8–2.3 (2.4)	2.05	30

Dist., Mokhovoe, *Q. robur*, 24.VII.2011 *Volobuev* (LE 314057*); Sverdlovsky Dist., Maryevka, *Betula pendula*, 1.IX.2012 *Volobuev* (LE 314055*); Uritsky Dist., Naryshkino, *B. pendula*, 6.X.2012 *Volobuev* (LE 292194*), *Q. robur*, 25.VI.2011 *Volobuev* (LE 314054*), 6.X.2012 *Volobuev* (LE 314053*). Primorie Reg.: Ternei Dist., Maisa, hardwood stump, 9.IX.1990 *Larsson 7182* (GB), *Alnus* sp. (?), 12.IX.1990 *Larsson 7447* (GB), Blagodatnoe, *Alnus* sp., 23.IX.1990 *Larsson 8140* (GB). Tuva: Turgen, *Larix sibirica* (charred corticated log), 23.VIII.2014 *Kotiranta 26776** (H). Spain. Burgos: Ordun, *Fagus sylvatica*, 12.XI.1977 *Ryvarden 15329* (O, H). Santander: Cavadonga, *Sambucus*, 14.IX.1977 *Ryvarden 15365* (O, H). Ukraine. Donetsk Reg.: Slovyansk Dist., Pyskunkivka, *Salix alba*, 20.XI.2010 *Akulov* (CWU 4704*). USA. Massachusetts: Hampshire Co., South Hadley, decayed wood, 4.V.2013 *Miettinen 16083** (H); Worcester Co., Holden, cut bole, 26.IX.2011 *Miettinen 14813.2** (H), Worcester, *?Acer saccharum*, 8.IX.2013 *Miettinen 16834* (H), *Populus tremuloides*, 5.X.2013 *Miettinen 17267.4* (H), *Quercus* sp., 6.X.2013 *Miettinen 17272** (H), *Acer* sp., 26.X.2014 *Miettinen 19035* (H). Michigan: Barry Co., Yankee Springs, *Quercus* sp., 3.IX.1955 *Cain* (H ex TRTC 31857). Tennessee: Cocke Co., Cosby, decayed wood, 13.VII.2004 *K.H. Larsson 12198* (GB), 14.VII.2004 *K.H. Larsson 12216* (GB), 17.VII.2004 *K.H. Larsson 12282**, *12297** (GB).

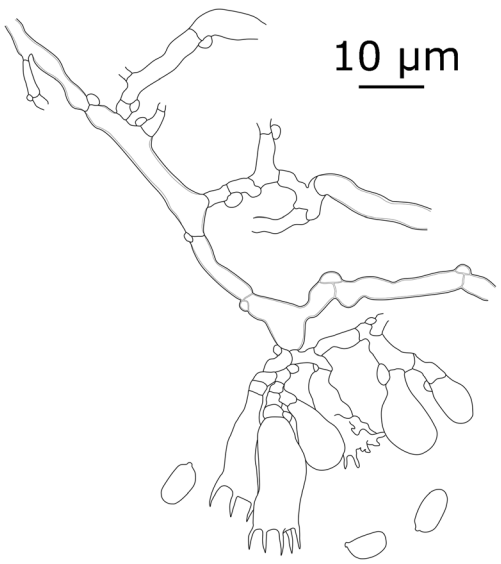

Fig. 7 Microscopic structures of *S. jacksonii* (Svantesson 699): hyphae, hymenial cells, and basidiospores

Sertulicium jacksonii (Liberta) Spirin & K.H. Larss., **comb. nov**.—Figs. 7 and 10

MB 833944

≡ *Paullicorticium jacksonii* Liberta, Brittonia 14: 223, 1962. Holotype. Canada. Ontario: York, Maple, decayed wood, 11.IX.1943 *Jackson* (TRTC 18722, studied).

Basidiocarps effused, pruinose, hardly visible by the naked eye, 0.02–0.03 mm thick. Hymenial surface whitish, smooth or porulose. Margin indistinct.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae sparse, randomly arranged, slightly to moderately thick-walled, branched mostly at sharp angles, often anastomosing, (2.2–) 2.3–6.4 (–6.8) μm in diam. (n = 68/5). Subhymenial hyphae thin- or slightly thick-walled, densely and randomly arranged, (2.0–) 2.1–3.8 (–4.0) μm in diam. (n = 100/5). Hyphidia occasionally present, simple, slightly projecting, 3–4 μm in diam. Basidia clavate, 4–6-spored, gradually tapering to the basal part, (11.6–) 12.2–23.8 (–24.7) × (5.8–) 5.9–9.3 (–9.4) μm (n = 72/4), a few pleural basidia seen. Basidioles broadly clavate to subglobose, (8.2–) 8.3–13.2 (–13.3) × (4.7–) 5.7–9.2 (–9.3) μm (n = 35/4). Basidiospores cylindrical to narrowly ellipsoid, straight or slightly curved, longest spores slightly tapering to the distal end, (5.1–) 5.2–8.2 (–8.6) × (2.7–) 2.8–4.1 (–4.2) μm (n = 170/6), L = 6.08–7.13, W = 2.99–3.66, Q = 1.79–2.39.

Remarks. *Paullicorticium jacksonii* was described from Canada but later rarely treated as a species of its own. Eriksson et al. (1978) placed *P. jacksonii* among the synonyms of *Sistotremastrum niveocremeum*, and the species has been interpreted that way up to the present moment. Our data confirm that *P. jacksonii* is a good species belonging to *Sertulicium*. In addition to the type collection, we studied specimens from the USA and Europe.

Sertulicium jacksonii belongs to a difficult complex of extremely thin, conifer-dwelling species hardly distinguishable via morphological traits. Among them, *S. jacksonii* can be recognized by its wide subicular hyphae with variably thickened walls. Two similar-looking species, *Sertulicium vernale* and *S. lateclavigerum*, have narrower subicular hyphae than those of *S. jacksonii*. Additionally, *S. lateclavigerum* possesses narrower basidiospores than in the other two species (Table 2). However, the differences listed here were detected from a very restricted set of specimens. Further studies with broader sampling may improve our observations considerably. *Paullicorticium ansatum* Liberta, yet another morphologically similar although phylogenetically unrelated species, may be easily separated from *Sertulicium* spp. due to ansiform (loop-like) clamps and basidia with up to eight sterigmata.

Specimens examined. Italy. Trentino—Alto Adige: Bolzano, *Picea abies*, 30.VIII.1990 *Bernicchia 5464* (O ex HUBO). Norway. Oppland: Jevnaker, *P. abies*, 4.X.2011 *Svantesson 699** (O). Russia. Karelia: Medvezhiegorsk Dist., Krivozero, *P. abies*, 19.VI.1942 *Laurila 3256b* (H). Leningrad Reg.: Boksitogorsk Dist., Kolp', *P. abies*, 28.VII.2016 *Spirin 10425** (H). USA. New York: Essex Co., Arbutus Lake, *Abies* sp., 22.IX.2013 *Miettinen 17141** (H).

Sertulicium lateclavigerum (Boidin & Gilles) Spirin & Viner, **comb. nov**.—Fig. 8

MB 833945

≡ *Sistotremastrum lateclavigerum* Boidin & Gilles, Bull. Soc. Mycol. France 110: 217, 1994. Holotype. France. Landes: Tartas, *Pinus pinaster* (fallen branch), 17.VI.1988 *Gilles 765** (LY-JB 13467, studied).

Basidiocarps effused, pruinose, rather loose or compact, covering a few cm, 0.02–0.05 mm thick. Hymenial surface cream-colored, smooth or porulose. Margin indistinct.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae sparse, randomly arranged, thin- or only slightly thick-walled, branched mostly at sharp angles, often anastomosing, (2.2–) 2.3–4.3 (–4.9) μm in diam. (n = 40/2). Subhymenial hyphae thin-walled (wall distinct), rather loosely and randomly arranged, (2.0–) 2.1–3.7 (–2.8) μm in diam. (n = 40/2). Cystidia occasionally present, thin-walled, easily collapsing, broadly clavate or subglobose, 19–33 × 9–16.5 μm. Hyphidia occasionally present, embedded, simple, 2–2.5 μm in diam. Basidia clavate, 4–6-spored, gradually tapering to the basal part, (9.3–) 9.9–20.7 (–21.2) × (4.4–) 4.8–9.3 (–11.1) μm (n = 40/2), a few pleural basidia seen. Basidioles broadly clavate to bladder-shaped or subglobose, (7.3–) 7.9–10.2 (–10.3) × (4.4–) 5.4–6.6 (–7.9) μm (n = 20/1). Basidiospores cylindrical to subfusiform, sometimes slightly curved, (4.3–)

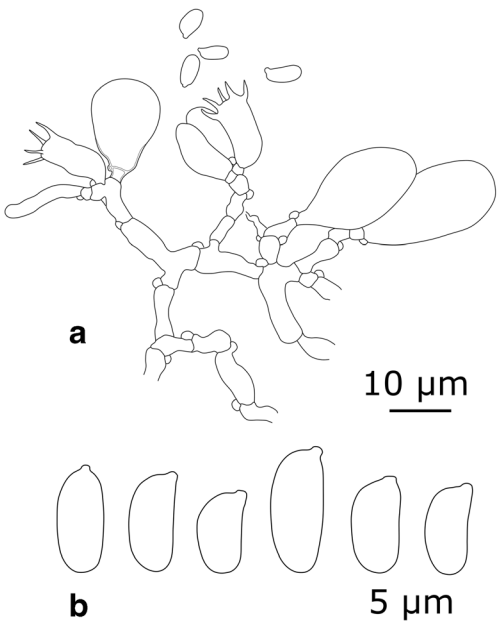

Fig. 8 Microscopic structures of *S. lateclavigerum* (holotype). **a** Hyphae and hymenial cells. **b** Basidiospores

4.6–7.2 (–7.3) × (2.1–) 2.2–3.2 μm (n = 60/2), L = 5.32–5.82, W = 2.57–2.84, Q = 2.05–2.09.

Remarks. *Sistotremastrum lateclavigerum* was described based on a single collection from France. The diagnostic features treated in the protologue were the bubble-like cystidia, basidia with up to 8 sterigmata and rather narrow and slightly curved basidiospores (Boidin and Gilles 1994). Sequences obtained from the holotype were published by Gruhn et al. (2018). They indicate that the species belongs to *Sertulicium* and it is not closely related to the similarly looking *S. jacksonii* and *S. vernale*. Morphological differences of *S. lateclavigerum* versus the two latter species are presented under *S. jacksonii*. *Paullicorticium allantosporum* J. Erikss. has basidiospores similar to *S. lateclavigerum*, (5.2–) 5.3–7.2 × (2.3–) 2.4–3.2 (–3.3) μm (n = 30/1), L = 6.10, W = 2.79, Q = 2.20, but they are more clearly curved and have large oil droplets in the cytoplasm. Moreover, basidia of *P. allantosporum* are 6–8-sterigmatic, with a clearly contracted and more or less sinuous basal part.

We studied the holotype of *S. lateclavigerum* and observed basidia with 4–6 sterigmata only. In our opinion, the presence of globose or broadly clavate cystidia-like cells is insufficient as a single diagnostic character in *Sistotremastrum* s. l. We observed hymenial cells of the same shape in one collection of *S. jacksonii* (*Laurila 3256b*), in *S. niveocremeum* (*Van Autgaerden S-20*), as well as in three representatives of *Sistotremastrum* s. str. (holotype of *S. geminum* and two senescent collections of *S. mendax* and *S. vigilans*, respectively). On the other hand, another collection of *S. lateclavigerum* studied by us (*Spirin 13457*) is totally devoid of cystidia-like cells.

So far, *S. lateclavigerum* has been collected in France and Slovenia. However, environmental sequences in GenBank and UNITE point to a broader distribution area of this species. One of them came from Vietnam (MF942562) while the second (UDB051695) is from Estonia.

Specimens examined. Slovenia. Gorenjska: Mojstrana, Triglavska Bistrica, *P. abies*, 28.IX.2019 *Spirin 13457** (H).

Sertulicium niveocremeum (Höhn. & Litsch.) Spirin & K.H. Larss., **comb. nov**.—Fig. 10

MB 833946

≡ *Corticium niveocremeum* Höhn. & Litsch., Sitzungsb. Kaiserl. Akad. Naturwiss. Mat.-Naturwiss. Klasse I 117:1117, 1908. Holotype. Austria. Niederösterreich: Wien-Umgebung, Unter-Tullnerbach, *Fagus sylvatica*, 11.III.1905 *Höhnel* (W 16251, studied).

= *Galzinia vesana* Boidin & Gilles, Bull. Soc. Mycol. France 106: 158, 1990. Holotype. France. Landes: St. Perdon, *Quercus pedunculata*, 2.III.1989 *Gilles 828* (LY-JB 13675, studied).

Basidiocarps effused, initially pruinose, later compact, covering several cm, 0.03–0.1 mm thick. Hymenial surface whitish to cream-colored or pale ochraceous, smooth or porulose. Margin first pruinose, later compact and sharply delimited.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae interwoven to subparallel, slightly thick-walled, branched mostly at right angles, (3.6–) 3.7–5.3 (–5.6) μm in diam. (n = 40/2); some hyphae inflated at septa up to 6 μm in diam. Subhymenial hyphae thin- or slightly thick-walled, densely arranged, some short-celled and slightly inflated, (2.2–) 2.3–4.3 (–4.5) μm in diam. (n = 80/4). Hyphidia occasionally present, embedded, simple, 2.5–4.5 μm in diam. Basidia clavate, 4–6-spored, gradually tapering to the basal part, (10.7–) 10.8–24.3 (–26.7) × (5.1–) 5.2–8.3 (–8.4) μm (n = 60/3), some basidia slightly thick-walled at the basal part. Basidioles broadly clavate to bladder-shaped or subglobose, (7.2–) 8.4–14.3 (–14.7) × (4.1–) 4.2–8.3 (–8.4) μm (n = 80/4). Basidiospores cylindrical, straight or slightly curved, (5.2–) 5.5–8.6 (–9.8) × (2.6–) 2.7–4.2 (–4.3) μm (n = 120/4), L = 6.55–7.46, W = 3.08–3.46, Q = 1.97–2.24.

Remarks. *Sertulicium niveocremeum* is distributed in temperate—boreal Eurasia. It inhabits angiosperm hosts, mainly still attached or recently fallen branches but it may occur also on rather rotten wood. For a long time, *S. niveocremeum* has been mixed up with another angiosperm-dwelling species, *S. granuliferum*; their differences are discussed under the latter species. We studied the type material and a recent collection of *Galzinia vesana* from France; in our opinion, it is merely a monstrous form of *S. niveocremeum* with unusually long basidia and basidiospores, as well as occasionally branched sterigmata. DNA data from recently collected specimens confirmed this synonymy. While introducing *G. vesana*, Boidin and Gilles (1990) referred to a description and illustration of *Galzinia* sp. from Sweden (Eriksson and Ryvarden 1975: 398) as another possible record of that species. We re-checked the specimen illustrated by Eriksson and concluded that it belongs to *Sertulicium*, being morphologically most similar to *S. niveocremeum*. However, its exact identity is still uncertain, and it is therefore treated as *Sertulicium* sp. 2 under Specimens examined.

Some specimens of *S. niveocremeum* collected in the winter or spring are dominated by four-sterigmatic basidia. Only a few 5–6-sterigmatic basidia were detected in such specimens after meticulous study. Moreover, these collections usually have longer basidiospores than in most other specimens of *S. niveocremeum* (in particular, reaching 14.5 μm long in specimen *Van Autgaerden S-20*) and thus can be mixed up with *Sistotremastrum vigilans*. The latter species, introduced below, has constantly four-sterigmatic basidia and it occurs exclusively on coniferous hosts while *S. niveocremeum* seems to be restricted to angiosperms.

Specimens examined. Belgium. Antwerpen: Zoersel, Zoerselbos, deciduous wood, 16.V.2019 *Van Autgaerden*

*S-20** (GENT). Oost-Vlaanderen: Kluisbergen, Kluisbos, deciduous wood, 20.II.2017 *Schoutteten 17-001* (GENT), 13.III.2017 *Schoutteten 17-202* (GENT). Finland. Varsinais-Suomi: Lohja, Tamminiemi, *Corylus avellana*, 5.XI.2020 *Spirin 14241* (H). Uusimaa: Helsinki, Veräjämäki, *Sorbus aucuparia* (?), 19.X.2011 *Miettinen 14925.3** (H). Etelä-Häme: Kangasala, Lorunkorpi, *Salix* sp., 23.III.2009 *Söderholm 4050** (H). France. Haut-Rhin: Sainte-Marie-aux-Mines, Freland, Le Limbach, *F. excelsior*, 12.X.2019 *Spirin 13566* (H). Pyrenées-Orientales: Argelès-sur-Mer, angiosperm (twigs), 2.XI.2008 *K.H. Larsson 13727** (GB). Italy. Emilia-Romagna: Bologna, *Quercus* sp., 3.XI.1983 *Bernicchia 1849* (O ex HUBO), 16.X.1984 *Ryvarden 22225* (O). Sardinia: Cagliari, 17.III.2003 *Arras 897* (H ex HUBO); Nuoro, *Quercus* sp., 30.III.2010 *Bernicchia 8593* (O ex HUBO). Russia. Krasnoyarsk Reg.: Turukhansk Dist., Bor, *Alnus sibirica*, 16.VIII.2013 *Kotiranta 26267** (H). Sakha Rep.: Nizhnekolymsk Dist., Tsherski, *Alnus fruticosa*, 18.VIII.1972 *Parmasto* (H ex TAAM 56632). Spain. Canary Islands: Tenerife, Las Mercedes, decayed wood, 18.I.1974 *Ryvarden 12639* (O, H). United Kingdom. England: Hampshire, New Forest Nat. Park, *F. sylvatica*, 5.II.1994 *Legon* (GB).

Sertulicium vernale Spirin & Volobuev, **sp. nov**.—Fig. 9 MB 833947

Holotype. Finland. Etelä-Häme: Kangasala, Pikku-Salmus, 61.4138° 23,9275° ±300 m, moist depression in rather old *Picea* forest, on a fallen, decorticated *Picea abies*, 10.V.2007 *Söderholm 3886** (H 6003442, isotype—LE).

Etymology. *Vernalis* (Lat., adj.)—vernal, occurring in the spring.

Basidiocarps effused, pruinose, rather loose, covering a few cm, 0.02–0.04 mm thick. Hymenial surface greyish, smooth or porulose. Margin indistinct.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae sparse, randomly arranged, slightly to moderately thick-walled, branched mostly at sharp angles, often anastomosing, (2.2–) 2.3–4.8 (–5.2) μm in diam. (n = 40/2). Subhymenial hyphae thin-walled (wall usually distinct), rather tightly and randomly arranged, (2.0–) 2.1–4.1 (–4.2) μm in diam. (n = 40/2), sometimes bearing bubble-like cells, 10–12 × 8–11 μm. Hyphidia rare, embedded, simple, 2.5–3.5 μm in diam. Basidia clavate, 4–6-spored, gradually tapering to the basal part, (11.2–) 11.8–27.4 (–37.2) × (5.0–) 5.1–7.2 (–7.3) μm (n = 44/2). Basidioles broadly clavate to bladder-shaped or subglobose, (6.0–) 6.9–10.2 (–10.8) × (4.4–) 5.2–6.8 (–6.9) μm (n = 20/1). Basidiospores narrowly ellipsoid to broadly cylindrical, sometimes slightly curved, (5.7–) 5.8–8.2 (–8.3) × (2.8–) 2.9–3.8 (–3.9) μm (n = 60/2), L = 6.90–7.02, W = 3.28–3.31, Q = 2.09–2.15.

Remarks. *Sertulicium vernale* is morphologically very similar to *S. jacksonii*, and it can be differentiated from the latter species by its narrower subicular hyphae and longer basidia. The species is so far known from two localities in Finland and two environmental sequence from Sweden (AY805625—Menkis et al. 2004) and CO, USA (JX136434—Huffman et al. 2013). The North American sequence is slightly different (2 bp) from the two European ones, and it may still belong to an undescribed sibling species.

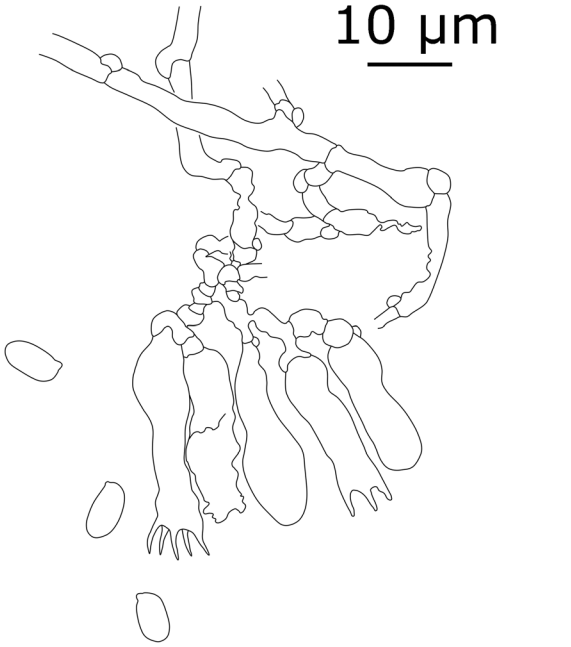

Fig. 9 Microscopic structures of *S. vernale* (holotype): hyphae, hymenial cells, and basidiospores

Specimens examined. Finland. Varsinais-Suomi: Lohja, Tamminiemi, *P. abies*, 5.XI.2020 *Spirin 14244* (H).

Sistotremastrum J. Erikss., Symb. Bot. Upsalienses 16 (1): 62, 1958.

Basidiocarps effused, thin to rather substantial (up to 0.2 mm thick), pruinose to waxy-compact. Hymenophore smooth, warted or odontioid-semiporoid. Hyphal structure monomitic; all hyphae clamped, CB (+), easily collapsing, in odontioid species with a more or less clear difference between trama and subhymenium. Cystidia absent in all but one species, hyphidia present, simple or accidentally branched. Basidia clavate or suburniform, with 2–4 or 4–6 sterigmata, usually collapsing at the apex, senescent basidia often slightly thick-walled at the base. Basidiospores thin-walled (but the wall distinct), narrowly ellipsoid or ovoid to cylindrical, inamyloid, acyanophilous, contents homogeneous and CB (+). On rotten wood of deciduous trees and conifers.

Generic type. *Sistotremastrum suecicum* Litsch. ex J. Erikss.

The genus is redefined here to exclude members of the *Sistotremastrum niveocremeum* complex subsumed under *Sertulicium*. Differences between the two genera are discussed above. Extending *Sistotremastrum* s. str. with a number of four-

sterigmatic taxa makes it difficult to delimit the genus from *Brevicellicium* and from smooth-spored *Trechispora* species. *Trechispora* differs by generally soft basidiocarps, short, often almost isodiametric subhymenial cells, and presence of ampullate septa on subicular hyphae. *Brevicellicium* species have similar subhymenial cells as in *Trechispora* but lack ampullate septa in the subiculum, which is poorly developed. Moreover, basidia in the four-sterigmatic *Sistotremastrum* spp. are more or less clearly suburniform, i.e., slightly constricted at the middle and narrowed at the apical part (except *S. vigilans* with exceptionally long, clavate-utriform basidia) while they are barrel-shaped or short-clavate in *Brevicellicium* and *Trechispora*.

All but one four-sterigmatic representatives of the genus treated below are distributed in tropical areas. However, two unnamed sequences (CMH343, GenBank KF800434; 6S1.10.S04, GenBank EF619877) originated from the eastern part of the USA (Fig. 4). This could point towards more undescribed taxa in the four-sterigmatic species complex distributed in geographic regions with a cooler climate.

Sistotremastrum aculeatum Miettinen & Viner, **sp. nov**.—Fig. 10

MB 833948

Holotype. Indonesia. Sumatera Barat: Kab. Lima Puluh Kota, Gunung Sago, -0.30585° 100.67762°, alt. 1400 m, lower montane rainforest, on a fallen log of dicot (decay stage 3/5), 25.VII.2009 *Miettinen 13799.1** (ANDA—holotype, H 7009306—isotype).

Etymology. *Aculeatus* (Lat., adj.)—aculeate.

Basidiocarps effused, first soft-floccose, then rather tough, covering several to tens of cm, 0.1–0.2 mm thick. Hymenial surface pale cream-colored to pale ochraceous, first warted, then odontioid, with irregularly arranged, sharp-pointed, partly fusing spines, 2–3 per mm, up to 2 mm long, or semiporoid, with shallow pores 0.5–1 per mm. Margin white to pale ochraceous, compact, in some portions with thin, white, pronounced hyphal strands. Smooth areas between spines fertile.

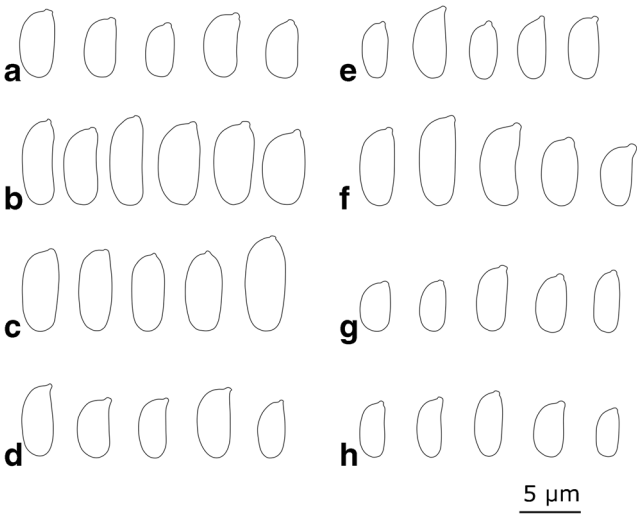

Fig. 10 Basidiospores of *Sertulicium* and *Sistotremastrum* spp. **a** *Sertulicium granuliferum* (Miettinen 14813.2). **b** *Sertulicium jacksonii* (three left—holotype, three right—Svantesson 699). **c** *S. niveocremeum* (holotype). **d** *Sistotremastrum aculeatum* (holotype). **e** *S. aculeocrepitans* (K.H. Larsson 16097). **f** *S. confusum* (holotype). **g** *S. denticulatum* (holotype). **h** *S. fibrillosum* (K.H. Larsson 16988)

Hyphal structure monomitic; hyphae clamped. Subicular hyphae unevenly thick-walled, (2.8–) 2.9–5.1 (–5.2) µm in diam. (n = 40/2), often in subparallel bundles. Tramal hyphae distinctly thick-walled, rather tightly arranged, interwoven to subparallel, sometimes glued together, (2.7–) 3.0–5.6 (–6.2) µm in diam. (n = 40/2). Subhymenial hyphae slightly thick-walled, short-celled, (2.3–) 2.4–4.2 (–4.6) µm in diam. (n = 40/2), rarely inflated up to 6 µm. Rhomboid or prismatic crystals occasionally present among subicular or tramal hyphae, up to 9 µm in widest dimension, solitary or in large groups. Hyphidia occasionally present, embedded or slightly projecting, simple, 2–3 µm in diam. Basidia suburniform, 2–4-spored, (7.3–) 7.7–12.2 (–12.3) × (3.3–) 3.4–4.5 (–5.2) µm (n = 30/2), senescent basidia slightly thick-walled at the basal part. Basidioles clavate to bladder-shaped, 5.4–8.2 × 3.2–4.3 µm (n = 10/1). Basidiospores cylindrical to narrowly ovoid, straight, (4.1–) 4.2–6.2 (–6.8) × (2.1–) 2.2–3.1 (–3.3) µm (n = 120/3), L = 4.98–5.07, W = 2.50–2.65, Q = 1.94–2.03.

Remarks. *Sistotremastrum aculeatum* seems to be widely distributed in South-East Asia from China to Sumatra. Morphologically, it is most similar to the South American *S. aculeocrepitans*. It differs from the latter species mainly by longer spines, which tend to fuse together and produce shallow, wide pores.

Specimens examined. China. Yunnan: Xishuangbanna, Mandian Waterfalls, hardwood (?), 17.VIII.2005 *Miettinen 10380.1** (H). Indonesia. Riau: Indragiri Hulu, Daerah Sungai Denalo, dead polypore, 2.VII.2004 *Miettinen 8829* (H). Thailand. Phang Nga: Kurabari, Kura Andaman Private Beach, hardwood, 3.II.2015 *Dunaev* KUN1105* (H). Singapore. Yishun, Nee Soon pipeline, hardwood, 17.III.2020 *Miettinen 23533** (SING, H).

Sistotremastrum aculeocrepitans Gruhn & Alvarado, Phytotaxa 379: 32, 2018.—Fig. 10

Basidiocarps effused, compact, covering several cm, 0.1–0.2 mm thick. Hymenial surface cream-colored to pale ochraceous, odontioid; spines densely arranged, 3–4 per mm, up to 0.3 mm long, sharp-pointed, sometimes fusing together and then fimbriate. Margin white to pale cream-colored, adnate, producing abundant thin, short, white hyphal strands. Smooth areas between spines fertile.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae interwoven, distinctly thick-walled, branched mostly at sharp angles, (3.4–) 3.8–5.7 (–6.0) µm in diam. (n = 20/1). Tramal hyphae distinctly thick-walled, densely arranged and

partly glued together, (2.8–) 2.9–4.8 (–5.2) μm in diam. (n = 20/1), in subhymenium more or less vertically oriented, thin- or slightly thick-walled, short-celled and slightly inflated, (2.9–) 3.1–4.8 (–4.9) μm (n = 20/1). Hyphidia abundant, embedded or projecting up to 20 μm, simple, 2–3.5 μm in diam. Basidia suburniform, 4-spored, (7.7–) 8.4–13.8 (–14.2) × (4.0–) 4.1–5.0 (–5.2) μm (n = 30/2). Basidioles clavate to bladder-shaped, 7–9 × 4–5 μm. Basidiospores cylindrical to narrowly ovoid, straight, a few of the longest spores slightly lacrymoid, (4.0–) 4.1–5.6 (–5.8) × (2.1–) 2.2–2.8 (–2.9) μm (n = 60/2), L = 4.44–5.10, W = 2.30–2.35, Q = 1.93–2.19.

Remarks. The species was introduced based on specimens from Martinique and French Guiana (Gruhn et al. 2018). We collected it in Brazil, and these specimens are the source of the present description. Differences of *S. aculeocrepitans* from *S. denticulatum* are treated under the latter species. Another similar-looking species from South America, *S. fibrillosum* Gruhn & Alvarado, has soft basidiocarps and densely arranged spines covering hyphal strands, and also considerably longer basidia. *Sistotremastrum aculeocrepitans* is reported here as new to Brazil.

Specimens examined. Brazil. Paraíba: Areia, Reserva Mata do Pau-Ferro, angiosperm, 28.IV.2013 *K.H. Larsson 16097** (URM, O). Pará: Belém, Museu Goeldi, Campus de Pesquisa, angiosperm, 25.XI.2013 *K.H. Larsson 16478** (MG, O).

Sistotremastrum confusum K.H. Larss. & Spirin, **sp. nov**.—Fig. 10

MB 833949

Holotype. Brazil. Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Barragem das Moças, -8.720420° -35.843436°, on rotten angiosperm wood, 20.IV.2013 *Larsson 16023** (URM, isotype—O).

Etymology. *Confusus* (Lat., adj.)—confusing.

Basidiocarps effused, soft, covering several cm, 0.04–0.07 mm thick. Hymenial surface whitish to cream-colored, smooth or irregularly tuberculate, accidentally cracking in old basidiocarps. Margin first arachnoid, with well-visible thin hyphal strands, later compact and rather clearly delimited.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae interwoven to subparallel, slightly thick-walled, irregularly branched, (2.2–) 2.3–4.2 (–4.8) μm in diam. (n = 40/2). Subhymenial hyphae thin- or slightly thick-walled, rather loosely arranged, some short-celled and slightly inflated, (2.4–) 2.6–4.2 (–4.8) μm in diam. (n = 40/2). Hyphidia rarely present, embedded or only slightly projecting, simple, 3–3.5 μm in diam. Basidia clavate, 4-spored, gradually tapering to the basal part, (12.2–) 13.1–25.0 (–28.8) × (4.3–) 4.4–6.2 (–6.3) μm (n = 22/2). Basidioles clavate to bladder-shaped, (7.3–) 7.4–11.8 (–13.0) × (4.2–) 4.3–5.3 (–6.0) μm (n = 20/2). Basidiospores cylindrical to narrowly ellipsoid or narrowly ovoid, (5.3–) 5.7–7.6 (–7.9) × 2.9–3.9 (–4.0) μm (n = 60/2), L = 6.54–6.57, W = 3.16–3.32, Q = 1.99–2.07.

Remarks. *Sistotremastrum confusum* is introduced here based on two sequenced collections from Brazil. Morphologically, it is most similar to *S. vigilans* distributed in Northern Hemisphere. The latter species has considerably larger basidia and basidiospores than those of *S. confusum*.

Specimens examined. Brazil. Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Barragem das Moças, angiosperm, 20.IV.2013 *K.H. Larsson 16004** (URM, O).

Sistotremastrum denticulatum Motato-Vásquez & Spirin, **sp. nov**.—Fig. 10

MB 833950

Holotype. Brazil. Saõ Paulo: Iguape, Juréia-Itatins Ecological Station, -24.417° -47.372°, fallen branch, 19.II.2017 *Motato-Vásquez 894** (SP 467087, isotype—H 7009716).

Etymology. *Denticulatus* (Lat., adj.)—denticulate.

Basidiocarps effused, soft, waxy covering several cm, 0.05–0.1 mm thick. Hymenial surface cream-colored to pale ochraceous, odontioid; spines densely arranged, 5–6 per mm, up to 0.5 mm long, rather blunt-pointed, sometimes fusing together and then fimbriate. Margin white to pale cream-colored, adnate, arachnoid, producing abundant thin, short, white hyphal strands. Smooth areas between spines fertile.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae interwoven to subparallel, distinctly thick-walled, branched mostly at sharp angles, (2.6–) 3.2–5.2 (–5.4) μm in diam. (n = 20/1). Tramal hyphae interwoven to subparallel, distinctly thick-walled, rather loosely arranged, (3.1–) 3.2–4.2 (–4.8) μm in diam. (n = 20/1), in subhymenium more or less vertically oriented, thin- or slightly thick-walled, mostly short-celled and slightly inflated, (2.2–) 2.3–3.8 (–4.1) μm (n = 20/1). Hyphidia abundant, mostly slightly projecting, simple, 2–3 μm in diam. Basidia suburniform to almost clavate, (1–) 2–4-spored, (6.7–) 7.2–12.2 (–12.3) × (3.7–) 3.8–4.8 (–5.0) μm (n = 20/1). Basidioles clavate to subglobose, (4.8–) 5.2–7.2 (–7.6) × (3.5–) 3.8–4.8 (–4.9) μm (n = 20/1). Basidiospores narrowly ellipsoid to broadly cylindrical, straight, a few of the longest spores somewhat fusiform, (3.9–) 4.0–5.3 (–5.4) × (2.0–) 2.1–3.0 (–3.1) μm (n = 30/1), L = 4.51, W = 2.48, Q = 1.83.

Remarks. *Sistotremastrum denticulatum* is morphologically most similar to *S. aculeocrepitans* but it has more densely arranged spines fusing together in characteristic fimbriate groups. Microscopically, these species are almost identical except for loosely arranged and not agglutinated hyphae in *S. denticulatum*. *Sistotremastrum fibrillosum* has spines not only on the hymenial surface but also on hyphal cords while *S. denticulatum* has sterile hyphal strands. The species is so far known only from the type locality in the southern part of Brazil.

Sistotremastrum fibrillosum Gruhn & Alvarado, Phytotaxa 379: 31, 2018—Fig. 10

Basidiocarps effused, soft, covering several cm, 0.05–0.1 mm thick. Hymenial surface cream-colored, odontioid; spines densely arranged, 6–9 per mm, up to 0.4 mm long, sharp-pointed, often fusing together in fascicles of 2–4, covering also hyphal strands. Margin white to pale cream-colored, floccose or radially fibrillose. Hyphal strands well developed, sometimes a few cm long and up to 0.5 mm thick.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae mostly subparallel, distinctly thick-walled, branched mostly at sharp angles, (3.3–) 3.6–6.2 (–7.1) µm in diam. (n = 20/1); some hyphae encrusted by densely distributed subglobose resinous globules. Tramal hyphae with unevenly thickened walls, rather loosely arranged, subparallel to interwoven, (3.2–) 3.3–4.3 (–4.6) µm in diam. (n = 20/1), in subhymenium more or less vertically oriented, thin- or slightly thick-walled, sometimes short-celled and slightly inflated, (1.7–) 2.0–3.2 (–3.6) µm (n = 20/1). Hyphidia present, embedded or projecting up to 20 µm, simple, 1.5–2 µm in diam. Basidia suburniform, 4-spored, (9.4–) 10.3–19.2 (–20.8) × (4.0–) 4.1–4.8 (–5.1) µm (n = 20/1). Basidioles clavate to bladder-shaped, 7–10 × 3.5–4.5 µm. Basidiospores cylindrical to narrowly ellipsoid, straight, (4.0–) 4.2–5.2 (–5.6) × (2.1–) 2.2–2.9 (–3.0) µm (n = 20/1), L = 4.72, W = 2.53, Q = 1.88, often glued together in large groups.

Remarks. The description above is based on a single specimen from Brazil. *Sistotremastrum fibrillosum* was originally introduced from four specimens collected in French Guiana (Gruhn et al. 2018). However, available DNA sequences show considerable variation, and this may indicate *S. fibrillosum* in the current sense is a collective species. More material is needed to find a more solid solution. Morphological differences of *S. fibrillosum* from *S. aculeocrepitans* detected in the same geographic region are treated under the latter species.

Specimens examined. Brazil. Pará: Melgaço, Caxiuanã, ICMBIO headquarter, angiosperm, 13.III.2015 *K.H. Larsson 16988** (MG 213771, O).

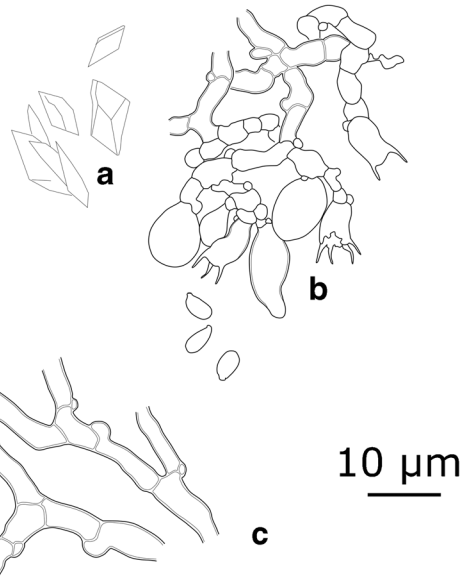

Fig. 12 Microscopic structures of *S. geminum* (holotype). **a** Crystals from subhymenial hyphae. **b** Subhymenial hyphae and hymenial cells. **c** Subicular hyphae

Sistotremastrum geminum Miettinen & Spirin, **sp. nov**.—Figs. 11 and 12

MB 833951

Holotype. Indonesia. Papua Barat: Manokwari Reg., Saukorem, Tamuk, -0.5832° 133.14845°, hilly lowland primary rainforest, on an uprooted *Intsia bijuga* (150 cm in diameter, decay stage 1-4/5), 30.X.2010 *Miettinen 14333.2** (MAN, isotype—H7009307).

Etymology. *Geminus* (Lat., adj.)—similar.

Basidiocarps effused, soft-floccose, covering several cm, 0.07–0.1 mm thick. Hymenial surface pale cream-colored, grandinioid, with irregularly arranged, obtuse warts 7–8 per mm. Margin pale cream-colored, floccose, partly detaching. Hyphal strands abundant in the underlying substrate, white and richly branched. Smooth areas between warts fertile.

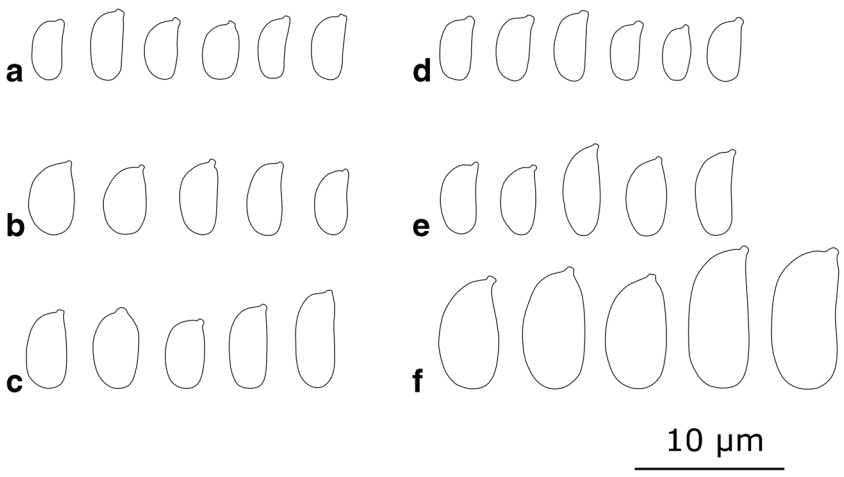

Fig. 11 Basidiospores of *Sistotremastrum* spp. **a** *S. geminum* (holotype). **b** *S. induratum* (holotype). **c** *S. mendax* (three left—holotype, three right—Spirin 10060). **d** *S. rigidum* (holotype). **e** *S. suecicum* (holotype). **f** *S. vigilans* (three left—Spirin 10097, two right—holotype)

Hyphal structure monomitic; hyphae clamped. Subicular hyphae interwoven to subparallel, slightly thick-walled, (2.3–) 2.8–4.8 (–5.2) μm in diam. (n = 20/1). Tramal hyphae thin-walled, rather loosely arranged, interwoven, as a rule short-celled and more or less distinctly inflated, (3.0–) 3.1–4.8 (–6.2) μm in diam. (n = 20/1). Subhymenial hyphae thin-walled, easily collapsing, often short-celled and slightly inflated or twisted, (2.2–) 2.3–3.4 (–3.7) μm in diam. (n = 20/1). Hyphal ends at spine tips thin-walled, short-celled, with occasional short side branches, 3–5 μm in diam., usually encrusted by solitary rhomboid crystals or solid crystalline shields. Cystidia unevenly distributed, thin-walled, varying from obtuse-clavate to subglobose, mostly enclosed, 11–22 × 6.5–9.5 μm. Hyphidia present, embedded or slightly projecting, simple, 2–3 μm in diam. at the apex, sometimes swollen at the base up to 4 μm in diam. Basidia suburniform, 4-spored, (7.8–) 8.0–11.2 (–11.8) × (3.6–) 3.7–4.4 (–4.6) μm (n = 20/1), senescent basidia slightly thick-walled at the basal part. Basidioles bladder-shaped to subglobose, (4.8–) 4.9–6.8 (–7.2) × (3.6–) 3.9–4.7 (–5.3) μm (n = 20/1). Basidiospores cylindrical to narrowly ellipsoid, straight to slightly curved, (3.8–) 3.9–5.2 (–5.5) × (1.9–) 2.0–2.6 (–2.9) μm (n = 30/1), L = 4.28, W = 2.24, Q = 1.92.

Remarks. Hymenophore with short warts (as opposed to long spines) and thin-walled, loosely arranged tramal hyphae differentiate *S. geminum* from other four-sterigmatic representatives of the genus treated here. The species is so far known only from the type locality in New Guinea.

Sistotremastrum induratum Spirin, **sp. nov**.—Fig. 11

MB 833952

Holotype. USA. Washington: Pend Oreille Co., Muskegon Lake, 48.7923° -117.044°, *Abies grandis*, 16.X.2014 *Spirin 8598** (H 7009717).

Etymology. *Induratus* (Lat., adj.)—hardening.

Basidiocarps effused, initially pruinose, later compact, covering several cm, 0.03–0.1 mm thick. Hymenial surface whitish to cream-colored, smooth or porulose. Margin first pruinose, later compact and rather sharply delimited. Hyphal strands present in subiculum of vigorously growing specimens, tough and well-differentiated.

Hyphal structure monomitic; hyphae clamped. Hyphae in strands densely arranged and partly agglutinated, more or less parallel, unevenly thick-walled, 5–6 μm in diam. Subicular hyphae interwoven to subparallel, unevenly thick-walled, branched mostly at right angles, (2.7–) 2.8–4.5 (–4.7) μm in diam. (n = 20/1). Subhymenial hyphae thin- or slightly thick-walled, densely arranged, some short-celled and slightly inflated, (2.8–) 3.0–4.8 (–5.0) μm in diam. (n = 40/2). Hyphidia occasionally present, embedded, simple, 3–5 μm in diam. Basidia clavate, 4–6-spored, gradually tapering to the basal part, (13.6–) 14.0–22.8 (–24.0) × (5.1–) 5.2–6.3 (–6.8) μm (n = 20/1). Basidioles clavate to bladder-shaped, (9.8–) 10.2–15.9 (–16.0) × (3.8–) 3.9–5.3 (–5.7) μm (n = 20/1). Basidiospores broadly cylindrical to narrowly ovoid, rarely ellipsoid, (4.0–) 4.1–5.3 (–5.8) × (2.5–) 2.6–3.1 (–3.2) μm (n = 60/2), L = 4.37–4.73, W = 2.79–2.86, Q = 1.53–1.70.

Remarks. *Sistotremastrum induratum* has so far been detected in two localities in the North American North-West. It is most similar to the European *S. mendax* but it has on average shorter basidia and basidiospores, as well as stable differences in ITS sequences. Distribution areas of the two species seem not to overlap.

Specimens examined. USA. Washington: Jefferson Co., Hoh River, *Picea sitchensis*, 20.X.2014 *Spirin 8804** (H).

Sistotremastrum mendax Spirin & Volobuev, **sp. nov**.—Figs. 5 and 11

MB 833953

Holotype. Norway. Telemark: Nome, Mørkvasslia Nat. Res., 59.288644° 8.865084°, rotten log of *Picea abies*, 23.IX.2003 *K.H. Larsson 12022** (GB).

Etymology. *Mendax* (Lat., adj.)—deceptive.

Basidiocarps effused, initially pruinose, later compact, covering several cm, 0.05–0.2 mm thick. Hymenial surface whitish grey to cream-colored or pale ochraceous, smooth or porulose, accidentally cracking only in very old basidiocarps. Margin first pruinose, later compact and rather sharply delimited. Hyphal strands present in subiculum of vigorously growing specimens, normally detectable by the naked eye.

Hyphal structure monomitic; hyphae clamped. Hyphae in strands densely arranged, parallel, slightly thick-walled, 1.5–2.5 μm in diam. Subicular hyphae interwoven to subparallel, slightly thick-walled, irregularly branched, (3.1–) 3.7–6.2 (–6.3) μm in diam. (n = 20/1). Subhymenial hyphae thin- or slightly thick-walled, densely arranged, some short-celled and slightly inflated, (2.2–) 2.3–4.2 (–4.3) μm in diam. (n = 50/3). Hyphidia rarely present, embedded, simple, 3–4 μm in diam. Basidia clavate, 4–6-spored, gradually tapering to the basal part, (11.4–) 11.7–27.2 (–27.3) × (4.6–) 4.8–6.6 (–7.2) μm (n = 50/3). Basidioles clavate to bladder-shaped, (7.2–) 8.2–13.8 (–15.3) × (4.2–) 4.3–6.2 (–6.5) μm (n = 20/2). Basidiospores narrowly ellipsoid to broadly cylindrical, some narrowly ovoid, (4.0–) 4.2–7.0 (–7.2) × (2.4–) 2.5–3.5 (–3.6) μm (n = 180/6), L = 4 75–5.71, W = 2.76–3.09, Q = 1.71–1.95.

Remarks. The species is introduced here as a sibling of *S. suecicum* occurring on wood of *Picea* in Europe. It differs from *S. suecicum* s. str. in having broader basidiospores and much better developed and easily observable hyphal strands in subiculum. Moreover, mature basidiocarps of *S. suecicum* are cracking in a characteristic way while they mostly stay continuous in *S. mendax* (Fig. 2). The host preference alone is not enough to recognize these species because *S. suecicum* sometimes occurs on spruce, as well as other coniferous trees. The

North American *S. induratum* has on average shorter basidia and basidiospores than *S. mendax* (Table 2).

According to our observations, *S. mendax* prefers old-growth spruce-dominated forests subjected to minimal (if any) logging activity. Further ecological studies are needed to confirm these observations.

Specimens examined. Czech Republic. South Bohemia Reg.: Boubín Nat. Res., *P. abies*, 29.X.2011 *Vlasák 1110/14.1* (H). Finland. Etelä-Karjala: Miehikkälä, Kaitai, *P. abies*, 3.VIII.1976 *Fagerström* (H). Satakunta: Lamppi, *P. abies*, 31.VIII.1939 *Laurila* (H). Norway. Sør-Trøndelag: Neadalen, Tydal, *P. abies*, 24.IX.2011 *J. Nordén 9579** (O). Poland. Podlasie: Hajnówka, Bialowieza NP, *P. abies*, 23.IX.2019 *Miettinen 22476** (H). Russia. Karelia: Medvezhiegorsk Dist., Krivozero, *P. abies*, 7.VI.1942 *Laurila 3251a, 3258* (H). Leningrad Reg.: Boksitogorsk Dist., Chagoda, *P. abies*, 9.V.2018 *Spirin 11887* (H), Kolp', *P. abies*, 8.V.2016 *Spirin 10057, 10060* (H), 9.V.2016 *Spirin 10086* (H); Podporozhie Dist., Oksboloto, *P. abies*, 27.V.2017 *Spirin 11223* (H), Vazhinka, *P. abies*, 21.V.2016 *Spirin 10107* (H), 4.VI.2016 *Spirin 10151* (H), 21.VI.2016 *Spirin 10226* (H), 26.V.2017 *Spirin 11208* (H), *Miettinen 20946** (H), 14–15.X.2017 *Spirin 11699, 11738* (H). Sweden. Värmland: Torsby, *P. abies*, 5.X.2010 *J. Nordén 7350* (O).

Sistotremastrum rigidum Motato-Vásquez & Spirin, **sp. nov**.—Fig. 11

MB 833954

Holotype. Brazil. Saõ Paulo: Trilha do Mirante, Serra do Mar State Park, -23.983° -46.7467°, fallen log, 17.XI.2016 *Motato-Vásquez 833** (SP 466010, isotype—H).

Etymology. *Rigidus* (Lat., adj.)—rigid, tough.

Basidiocarps effused, crustaceous, tough, covering several cm, 0.05–0.08 mm thick. Hymenial surface almost white to cream-colored, smooth. Margin white, indistinctly fimbriate, adnate, occasionally with short hyphal strands.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae tightly glued together, interwoven to subparallel, thick-walled, hardly visible, 2–4 μm in diam. Subhymenial hyphae slightly to distinctly thick-walled, densely arranged and partly glued together, some short-celled and slightly inflated, (2.0–) 2.1–3.0 (–3.2) μm in diam. (n = 20/1). Hyphidia rarely present, mostly embedded, simple, 2–2.5 μm in diam. Basidia suburniform to almost clavate, 4-spored, (7.7–) 9.2–14.3 (–16.2) × (4.6–) 4.8–6.6 (–7.2) μm (n = 20/1), senescent basidia slightly thick-walled at the basal part. Basidioles rare, subglobose, 5–6 × 4–5 μm. Basidiospores cylindrical to broadly cylindrical, (3.8–) 4.0–5.1 (–5.2) × 2.0–2.5 (–2.7) μm (n = 30/1), L = 4.44, W = 2.22, Q = 2.01.

Remarks. Basidiocarps of *S. rigidum* are exceptionally tough due to densely arranged and partly agglutinated hyphae, making the structure resemble species of *Phlebia* s.l. However, none of the latter ones forms hyphal strands or has suburniform basidia with slightly but distinctly thickened walls. Another four-sterigmatic species with smooth hymenophore, *S. confusum*, occurs in Brazil. However, it differs from *S. rigidum* in having soft basidiocarps and larger basidia and basidiospores.

Sistotremastrum suecicum Litsch. ex J. Erikss., Symb. Bot. Upsalienses 16 (1): 62, 1958—Figs. 5 and 11

Holotype. Sweden. Upland: Uppsala, Bondkyrka, "on the under-side of coniferous fencing-material, lying in a wet spot" [*Pinus sylvestris*—identified by Pirkko Harju, H], 4.I.1933 *Lundell* (Fungi Exsiccati Suecici #464) (S F204406, studied).

Basidiocarps effused, initially pruinose, later waxy, covering several cm, 0.05–0.2 mm thick. Hymenial surface whitish to cream-colored or pale ochraceous, smooth or porulose, in older basidiocarps often cracking into small irregular patches. Margin first pruinose, later compact and rather sharply delimited. Hyphal strands present in basal layer of vigorously growing specimens.

Hyphal structure monomitic; hyphae clamped. Hyphae in strands densely arranged, parallel, slightly thick-walled, 1.5–2.5 μm in diam. Subicular hyphae interwoven to subparallel, slightly thick-walled, branched mostly at right angles, (3.8–) 3.9–5.8 (–6.2) μm in diam. (n = 40/2). Subhymenial hyphae thin- or slightly thick-walled, densely and randomly arranged, in subhymenium more or less vertically oriented, some short-celled and slightly inflated, (2.2–) 2.3–4.1 (–4.2) μm in diam. (n = 100/5). Hyphidia occasionally present, embedded or projecting (especially in young specimens) up to 15 μm above hymenial layer, simple, 2–4 μm in diam. Basidia clavate, 4–6-spored, gradually tapering to the basal part, (10.6–) 12.8–26.7 (–26.8) × (4.1–) 4.2–6.2 (–6.3) μm (n = 80/5). Basidioles clavate to bladder-shaped, (8.3–) 8.6–14.2 (–15.1) × (3.3–) 3.8–5.2 (–5.8) μm (n = 20/1). Basidiospores cylindrical to narrowly ovoid, (4.1–) 4.2–6.2 (–6.3) × (2.1–) 2.2–3.1 (–3.2) μm (n = 180/6), L = 4.56–5.55, W = 2.42–2.80, Q = 1.83–2.06.

Remarks. *Sistotremastrum suecicum* was described from Sweden (Eriksson 1958) and has so far been treated in a collective sense, i.e., the name has been used for all collections from coniferous hosts. According to our results, *S. suecicum* occurs almost exclusively on *Pinus* spp., like the so-called kelo trees in North Europe (Niemelä et al. 2002). It is considered an indicator species of old pine forests of high conservation value in Finland (Niemelä 2016). Most specimens from other gymnosperm hosts belong either to *S. mendax* (in Europe) or to *S. induratum* (in the North American North-West). Differences of *S. suecicum* from the latter two species are discussed under *S. mendax*. The species forms basidiocarps throughout the year.

An ITS sequence of *S. suecicum* UC2022903 found on pine wood in California (GenBank KP814148) is clearly different from the rest of the pine-dwelling collections and seemingly representing a species of its own. We leave this problem until more material from the US Pacific will be available. Future studies should elucidate if *S. suecicum* s. str. is also present in this geographic area or if its distribution in North America is limited to the east of the Rocky Mountains.

Specimens examined. Canada. British Columbia: Fraser—Fort George Reg. Dist., Jackman Flats Prov. Park, *Pinus contorta*, 25.VII.2015 *Spirin 8932** (H). Nova Scotia: Kentville, Ravine, *Pinus resinosa*, 8.VIII.1954 *Harrison* (H ex DAOM 52237). Finland. Varsinaissuomi: Parainen, Kuggö, *P. sylvestris*, 24.X.2009 *Kunttu 5959** (H). Pohjois-Savo: Heinävesi, Vihtarinniemi, *P. sylvestris*, 2.X.2006 *Miettinen 11044.1** (H). Inarin Lappi: Inari, Piekanavaara, *P. sylvestris*, 28.VIII.2008 *Miettinen 13310.1* (H). Russia. Arkhangelsk Reg.: Krasnoborsk Dist., *P. sylvestris*, 5.VIII.2013 *Kotkova* (LE 295792*). Krasnoyarsk Reg.: Turukhansk Dist., Bor, *P. sylvestris*, 24.VIII.2013 *Kotiranta 26451* (H). Leningrad Reg.: Boksitogorsk Dist., Chagoda, *P. sylvestris*, 10.V.2018 *Spirin 11888, 11890* (H), Shidrozero, *P. sylvestris*, 14.VIII.2014 *Spirin 6974* (H); Podporozhie Dist., Kurba, *P. sylvestris*, 19.IX.2009 *Spirin 3236* (H), Vazhinka, *P. abies*, 14.X.2017 *Spirin 11697* (H). Nizhny Novgorod Reg.: Arzamas Dist., Pustyn', *P. sylvestris*, 13.VIII.2015 *Spirin 9227, 9233* (H). Sweden. Jämtland: Härjedalen, Glumtjärnarna, *P. sylvestris*, 14.VIII.2011 *Miettinen 14550.1** (H). Ångermanland: Resele, Vignäsbodarna, *P. abies* (?), 28.VIII.2002 *K.H. Larsson 11849** (GB). Jämtland: Härjedalen, Ransjön, *P. sylvestris*, 14.VIII.2011 *Miettinen 14548* (H). USA. Massachusetts: Worcester Co., Holden, fallen branch, 26.IX.2011 *Miettinen 14829** (H), *Tsuga canadensis*, 21.IV.2013 *Miettinen 16061** (H), *Tsuga*/*Pinus* sp., 27.VII.2013 *Miettinen 16618** (H).

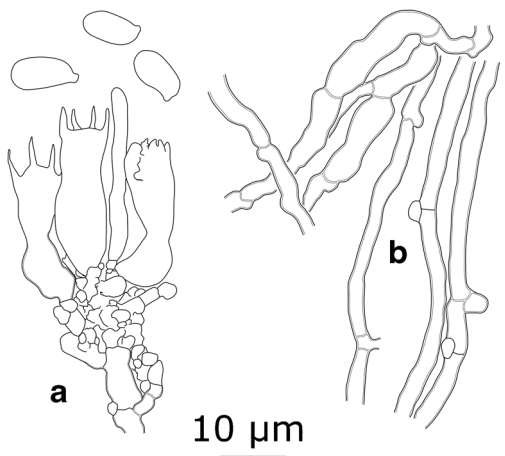

Fig. 13 Microscopic structures of *S. vigilans* (holotype). **a** Subhymenial hyphae and hymenial cells. **b** Subicular hyphae

Sistoremastrum vigilans K.H. Larss. & Spirin, **sp. nov**.—Figs. 11 and 13

MB 833955

Holotype. Norway. Vestfold: Stokke, Melsomvik, 59.22541° 10.35202°, rotten log of *Picea abies*, 30.IV.2011 *Fonneland 2011-78** (O).

Etymology. *Vigilans* (Lat., adj.)—vigilant.

Basidiocarps effused, compact, covering several cm, 0.05–0.2 mm thick. Hymenial surface white to cream-colored or pale ochraceous, first smooth, in older basidiocarps irregularly cracking and unevenly tuberculate. Margin first pruinose, later compact and sharply delimited. Hyphal strands often present, well-developed, white, occurring in subiculum and sometimes in the underlying substrate.

Hyphal structure monomitic; hyphae clamped. Subicular hyphae in parallel bundles or interwoven, with unevenly thickened walls, randomly branched, some tortuous, with occasional oil-drops, (3.1–) 3.2–5.6 (–5.7) µm in diam. (n = 60/3), in older parts with bubble-like inflations 7–10 µm in diam. Subhymenial hyphae thin- or slightly thick-walled, densely arranged, some short-celled and slightly inflated, (2.0–) 2.2–4.2 (–5.0) µm in diam. (n = 60/3). Hyphidia occasionally present, embedded or projecting up to 20 µm, simple or with accidental side branches, 1.5–5 µm in diam. Basidia clavate to utriform, 4-spored, with widened or tapering bases, (11.3–) 11.4–34.1 (–38.2) × (5.3–) 5.4–8.0 (–8.1) µm (n = 50/3). Basidiospores narrowly ellipsoid to long cylindrical, straight or slightly curved, a few lacrymoid or sigmoid, (6.1–) 6.3–11.2 (–11.4) × (3.0–) 3.1–5.4 (–6.2) µm (n = 150/5), L = 7.43–9.95, W = 3.64–4.69, Q = 1.81–2.22.

Remarks. *Sistotremastrum vigilans* is the only four-sterigmatic species of the genus so far detected in temperate and boreal forests of the Northern Hemisphere. It occurs on coniferous hosts, either late in the season or in spring, and this might have been a reason for overlooking it. The species is rare and tends to occur in rather old forests with large-diameter dead wood.

Sistotremastrum vigilans has the largest basidiospores in the genus and thus it can be mistaken for a *Hyphoderma* s. l. species. Basidia of highly variable size, basidiospores with homogeneous contents (not guttulate as in *Hyphoderma*) and slightly thicker walls, as well as occasionally inflated subicular hyphae are the most reliable traits for a morphological identification of this species. The well-developed hyphal strands (if present) are another clue to recognizing *S. vigilans*.

Specimens examined. Canada. Québec: Outaouais, Gatineau Nat. Park, *Abies balsamea*, 14.X.1967 *Eriksson 9106* (GB, K), conifer, 15.X.1967 *Eriksson 9140*, *9270*, *9279* (GB, K), *A. balsamea*, 22.X.1967 *Eriksson 9281* (GB, K). Finland. Uusimaa: Helsinki, Laajasalo, *P. abies*, 25.XI.1934 *Häyrén* (H), Haltiala, *P. abies*, 20.XII.2020 *Miettinen 24513* (H). Satakunta: Vuorijärvi, *P. abies*, 6.IX.1937 *Laurila* (H). Norway. Vestfold: Stokke,

Melsomvik, *P. abies*, 30.IV.2011 *Fonneland 2011-77* (O). Russia. Leningrad Reg.: Podporozhie Dist., Vazhinka, *P. abies*, 21.V.2016 *Spirin 10097** (H), 22.V.2016 *Spirin 10135* (H). USA. Washington: Jefferson Co., Hoh River, *Tsuga heterophylla*, 20.X.2014 *Spirin 8778** (H).

Discussion

In this paper, we present the most comprehensive study of *Sistotremastrum* to date. *Sistotremastrum* sensu lato now holds 18 species, which means that species number more than doubled. The original concept of *Sistotremastrum* (Eriksson 1958) contained only two species, *S. suecicum* and *S. niveocremeum*. However, with the much richer sampling available to us, the phylogenetic analyses prompted us to segregate the species around *S. niveocremeum* into the new genus *Sertulicium*.

Larsson (2007) showed that *Sistotremastrum suecicum* and *S. niveocremeum* belong in the Trechisporales forming a strongly supported sister clade to the rest of the order. Larsson (2007) named this clade the *Sistotremastrum* family while for the sister clade the name *Hydnodontaceae* is available. The same strongly supported topology was recovered by Gruhn et al. (2018) in a paper where two new *Sistotremastrum* species were introduced. In the present work, we were not able to generate high support values for the node connecting *Sistotremastrum* and *Sertulicium* (Fig. 1). The reason for this is unclear but probably depends on the generally high diversity of the nuclear ribosomal markers in Trechisporales. We think it is likely that the concept of *Sistotremastrum* family as defined by Larsson will survive, but the question can only be solved with sequences from an expanded set of genes.

Three species, *Sistotremastrum denticulatum*, *S. geminum*, and *S. rigidum*, are described based on single specimens. While we normally would avoid doing this, we found it justified in these cases. These three species are all well separated in ITS alignments and differs by 3.6%, 4.6%, and 9.0%, respectively, from their phylogenetically closest relatives (Fig. 1). Furthermore, all the close relatives of these single-specimen species are represented by multiple ITS sequences, increasing confidence that such big ITS differences represent inter- and not infraspecific variation. All these species are also morphologically clearly separable from their closest relatives. Lastly, we used distinct distribution areas as a criterion. Distribution areas of *S. denticulatum* and *S. rigidum* do not overlap with their closest relatives. Difference in distribution areas is not as clear in the case of *S. geminum* and its closest relative *S. aculeatum*, which are both found in South-East Asia. However, the latter has been found so far only west of Wallace's line (Sumatra and Asian mainland), while *S. geminum* east of it, in Australasia (New Guinea).

Other specimens examined

Brevicellicium exile. USA. Washington: Clark Co., Gifford Pinchot Nat. Forest, *T. heterophylla*, 11.X.2014 *Spirin 8370** (H).

B. olivascens. Russia. Nizhny Novgorod Reg.: Bogorodsk Dist., Krastelikha, *Q. robur*, 5.IX.2011 *Spirin 4446** (H). Sweden. Bohuslän: Restenäs, Ulvesund, decaying angiosperm branch, 3.X.1998, *Larsson 8571** (GB).

B. viridulum. Russia. Sakhalin: Uglegorsk Dist., Telnovskoe, *Alnus hirsuta*, 1.IX.2007 *Kotiranta 29271** (H).

Luellia cystidiata. Denmark. Jylland: Varde, Bordrup Klitplantage, *P. abies*, 6.X.2009 *Petersen & Læssøe 13875* (GB).

Paullicorticium allantosporum. Norway. Hedmark: Løten, Gitvola, *P. abies*, 26.IX.2018 *Spirin 12413* (H).

Pteridomyces galzinii. Italy. Tuscany: Arezzo, Camaldoli Nat. Res., *Polystichum aculeatum*, 17.XI.2010 *Bernicchia 8122** (GB).

Sertulicium aff. *granuliferum*. Kenya. Eastern Prov.: Meru, Chigora, decayed wood, 31.I.1973 *Ryvarden 3593* (O); Nyeri, Regati, decayed wood, 2.II.1973 *Ryvarden 9777* (O), *Ryvarden 9888* (O). Tanzania. Tanga Prov.: Tanga Dist., Amani, decayed wood, 18.II.1973 *Ryvarden 10575* (O, H).

Sertulicium sp. 1. Russia. Khabarovsk Reg.: Khabarovsk Dist., Ilga, *Corylus mandshurica*, 11.VIII.2012 *Spirin 5158** (H).

Sertulicium sp. 2. Sweden. Bohuslän: Säve, *P. sylvestris* (bark), 4.III.1973 *Arvidsson* (GB).

Suillosporium cystidiatum. Russia. Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Picea ajanensis*, 5.VIII.2011 *Spirin 3830** (H).

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Data availability DNA sequences used in the present study are available in GenBank. Alignments were deposited in TreeBASE. Fungal specimens are stored in public herbaria (as indicated under "Specimens examined").

Declarations

Ethics approval Not applicable

Conflict of interest The authors declare no competing interests.

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